

ECOLOGICAL MONOGRAPHS

Vol. 6

APRIL, 1936

No. 2

THE PARASITES OF SOME NORTH CAROLINA RODENTS

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THE PARASITES OF SOME NORTH CAROLINA RODENTS

INTRODUCTION

The parasites of rodents are of unusual interest. Probably because rodents are of small size and can be captured with comparative ease students of parasites have often examined them. Not only do many rodents carry infectious diseases but the damage they do to crops and forests results in losses of thousands of dollars annually. Rodents furnish very satisfactory material for the study of experimental parasitic infestations.

Fluctuations in the number of wild animals are of importance both in pure and applied ecology. These often result from epidemic diseases caused by animal parasites, bacteria, or fungi. Animal parasites usually are not fatal but may lessen the vitality so that infectious diseases are more serious.

PREVIOUS WORK

Wenyon (1926) has made a careful study of all protozoan parasites. Levine and Becker (1933) made a host and check list of the species of *EIMERIA* and this includes many rodent parasites.

Hall (1916) monographed the known nematodes from the orders Rodentia, Lagomorpha, and Hydracoidea. He described 34 species from North American rodents including 11 new species. Yorke and Maplestone (1926) included in their work on the "Nematode Parasites of Vertebrates" a list of all the known species of parasitic nematodes. The various trichostrongylids were treated by Nagaty (1932) who reduced the number of species found in rodents to five.

Several new species of tapeworms were reviewed by Stiles (1895). The cestode family Anoplocephalidae was reviewed thoroughly by Douthitt (1915) and Baer (1927). Meggitt (1924) monographed the cestodes of mammals and included a list of all known cestodes.

Trematodes are represented in very few species of North American rodents. The aquatic types such as the muskrat and the beaver are the only representatives which show an appreciable number of trematode species. These have been described by various authors. Barker (1915) in conjunction with various co-workers, and Price (1931) described the majority of the species from the muskrat.

The systematic classification of external parasites has been done by various specialists. Ferris has studied the Anoplura. The Acarina have been studied by Banks (1915) and Ewing (1922, 1925). The Ixodidae were monographed carefully by Nuttall, Warburton, and their associates (1908, 1911, 1915).

Baker (1904, 1905), Jordan and Rothschild have studied the fleas. Jordan (1933) reduced the numerous American species of *CERATOPHYLLUS* by creating new genera for many of the species. Rocky Mountain spotted fever has stimulated work upon the external parasites of mammals, especially in the Bitter Root Valley, Montana. The fleas of the rodents were studied by Dunn and Parker (1925) and *Derma-centor andersoni* Stiles was surveyed by Cooley (1915, 1932), and Hooker, Bishopp, and Wood (1912).

The pathological and economic significance of special groups of rodents has stimulated parasitological research on such animals. It is inadvisable to discuss the results of such work. However, a cursory summary of the major works is necessary. The helminth parasites of the rat were carefully surveyed by Oldham (1932). The intestinal protozoa of the rat were studied by Hegner (1929) and Kofoed, McNeil and Bonestell (1933). The presence of *Gongylonema neoplasticum* (Fibiger and Ditlevsen 1914) and *Apophallus donicum* (Skrjabin and Lindtrop 1919) in the rats of Washington is of significant interest (Price and Chitwood, 1932). The external parasites of the rat have been studied in various places. Fox and Sullivan (1925) have summarized the subject very well.

The genus *Citellus* has been studied intensively. The protozoans were covered very thoroughly by Becker (1926-1933) and co-authors and Henry (1932). The helminths were studied by MacLeod (1933). The genera *Lepus* and *Sylvilagus* have been studied rather intensively in various localities. A summary of rabbit parasites and diseases was compiled by Schwartz and Shook (1928, 1933). The parasites of the rabbits of Canada were surveyed by Boughton (1932). The study of rabbits in Arizona was undertaken by Vorhies and Taylor (1933) and those of Oklahoma by Ward (1934). Weimer, Hedden and Cowdery (1934) made an investigation upon the helminth parasites of rabbits in West Virginia.

MATERIALS AND METHODS

A total of 287 rodents including 41 cottontail rabbits, 53 gray squirrels, 54 white-footed mice, 84 house mice and 55 brown rats were examined for parasites. The rabbits were collected from October, 1933 to August, 1934. The other rodents were examined from May, 1934 to April, 1935. All of the hosts were collected in Durham County and the majority of the forest dwellers from the Duke Forest.

The only animals obtained alive throughout the period of observation were the house mice, which were captured with box traps in various houses and buildings in Durham, North Carolina. The rabbits and squirrels were shot with a 0.12 gauge shotgun. The white-footed mice were captured with the use of snap-traps. They were collected within 9 to 14 hours after the baiting of the traps. Rats were captured alive during the summer months by

means of steel traps but these proved unsatisfactory during the fall and winter months when they were shot with a 0.22 rifle. The rats obtained during the summer months were collected from various meat and grocery establishments in Durham, N. C. Those shot were "dump" rats. When captured the animals were at once placed in tight cloth bags in order to prevent the escape of external parasites.

All of the animals with the exception of some of the squirrels, which were captured by a hired hunter, were removed to the laboratory and examined immediately for external parasites and protozoa. In some cases examination could not be completed immediately and the non-examined organs were placed in a cold room where the temperature remained at about 4° C.

In the laboratory hosts were removed from the cloth bags and combed carefully with a fine-tooth comb for external parasites. Fleas were killed with a chloroformed brush. Lice and mites were killed in hot 70 per cent alcohol. The cloth bag was then examined under a binocular microscope. All external parasites were preserved in 70 per cent alcohol and cleared in turpinol.

The host was skinned and blood and intestinal smears were made and examined for ten minutes each under high and low power objectives. Three fresh blood smears were obtained from the heart and liver. Three smears each were made from the stomach, duodenum, jejunum, ileum, caecum, colon, and rectum. The internal organs, the intercostal and diaphragm muscles were dissected under a binocular microscope and the parasites removed and washed in physiological salt solution. The muscles were also pressed between glass plates as an examination for trichina.

Protozoans were fixed in hot Bouin's fixative and stained in iron-alum haematoxylin. Nematodes were killed in 70 per cent alcohol and preserved in five parts of 70 per cent alcohol to one part of glycerin. Cestodes were allowed to die in tepid water to insure complete relaxation of the proglottids. Cestodes and trematodes were fixed and preserved in Conant's fixative of the following formula:

| | |
|---------------------------|------------|
| 50 per cent alcohol..... | 100.0 c.c. |
| Glacial acetic acid..... | 2.5 c.c. |
| 40 per cent formalin..... | 6.5 c.c. |

For microscopic examination and identification of the parasites cestodes were stained in Ehrlich's haematoxylin and trematodes in borax-carmin. They were mounted in damar. Nematodes were cleared in glycerin and examined.

The writer wishes to thank Dr. A. S. Pearse for the many helpful suggestions and criticisms given during the course of this work and the preparation of this manuscript. Thanks are also due to Dr. M. C. Hall for the use of the host catalogue of the Bureau of Animal Industry; to Dr. B. G. Chit-

wood, Dr. M. Skinker, Dr. H. E. Ewing and Dr. A. D. Shaftesbury for the identification of the nematodes, cestodes, mites, and lice, and fleas respectively; to Mr. Allen McIntosh for assistance in the preparation of the bibliography of parasites; to Dr. H. F. Prytherch, United States Bureau of Fisheries, Beaufort, North Carolina, for laboratory space, and to Mr. B. C. Shrapnel for assistance in the examination of some of the hosts.

HOSTS EXAMINED

After a preliminary survey of the rodents of North Carolina five were selected to study. These were species which varied in habits, size, and food and could be obtained in sufficient numbers to permit routine examinations throughout a year.

Sciurus carolinensis carolinensis Gmelin

The southern gray squirrel was selected for study as a comparatively large, arboreal mammal. The total length may be 250 cm.

Gray squirrels are active only during the day. They store up nuts, fruits, buds, seeds, and grains for times when food will be difficult to find. They do not hibernate although they may remain in the nest for long periods during inclement winter weather. They are strictly arboreal rodents and are not found away from forests.

The gray squirrel either builds a bulky nest of leaves and twigs in the crotch of a limb or else chooses a hollow in some rotted tree trunk. The young number from four to six and often two litters are raised a year.

Peromyscus leucopus leucopus (Rafinesque)

White-footed mice share with the meadow mice the distinction of being the commonest and most widely distributed of the North American small rodents. *Peromyscus leucopus leucopus* is a small rodent having a maximum length of 18 cm. with the tail less than half the total length. It frequents the cover of fallen logs, piles of rock, and other shelters such as are common in forests and brush lands. Occasionally it builds a nest in low bushes, or uses old nests made by birds. It is terrestrial, strictly nocturnal, and is active throughout the year. The food is almost strictly vegetarian. The number of young in a litter varies from three to seven but is usually four or five. There may be as many as four or five litters a year, hence young may be seen at almost any time.

Mus musculus musculus Linnaeus

This is the only species of the genus *Mus* which has established itself in North America. The maximum total length is 150 to 155 cm. While this mouse is more or less a "house" mouse it lives in open fields in many places. It is omnivorous but it is not as destructive as the rat.

Rattus norvegicus (Erxleben)

The brown, or Norway, rat has a maximum total length of 275 cm. It is perhaps the most thoroughly disliked of rodents. It frequently lives under filthy conditions, carries disease and is such a destructive creature that the hand of man has been set against it from time immemorial. The Norway rat is aggressive and so easily adapts itself to varying conditions that today it has a cosmopolitan distribution. It lives in great numbers in all large cities, on water-fronts, and is also widely spread over less inhabited districts, even frequenting fields and brushy areas where it finds favorable conditions.

Sylvilagus floridanus mollurus (Thomas)

The cottontail rabbit is a typical mammal of medium size and is widely distributed. In forested regions cottontail rabbits frequent only brushy areas among the trees, coming out to feed upon green vegetation in the late afternoon or early morning about the edges of fields or meadows. It is seldom seen in heavy stands of trees where there is no underbrush or an occasional glade. Cottontails are very prolific and in the warmer parts of their range young animals may be found during any month of the year. The production of several broods a year is general among representatives of this genus. The number of young in a litter varies from three to seven, with four as an average.

PARASITES WHICH INFESTED THE HOSTS EXAMINED

In this section the parasites found by the writer in each host are presented separately. The genus and species of the parasites, author and date of description, the average number of parasites per host, the percentage of hosts infested, and the part of the body which the parasite infests are given. Tables 1 to 5 present data by months for the various parasites.

SCIURUS CAROLINENSIS CAROLINENSIS Gmelin

CESTODA

1. Larval stage of *Taenia taeniaeformis* (Batsch 1786): 0.189, 1.89%; liver.

NEMATODA

2. *Longistriata hassalli* (Price 1925): 77.5, 92.45%; duodenum.

ARTHROPODA

ACARINA

3. *Atricholaelaps glasgowi* (Ewing 1925): 0.32, 13.2%; on skin.
4. *Ixodes hexagonus* (Leach 1815): 0.075, 5.66%; on skin.
5. *Trombicula* sp.: 6.35, 50.94%; on skin.

ANOPLURA

6. *Hoplopleura sciuricola* (Ferris 1921) : 3.81, 32.64% ; on skin.
7. *Neohaematopinus sciurinus* (Mjöberg) : 28.75, 50.94% ; on skin.

SIPHONAPTERA

8. *Orchopeas wickhami* (Baker 1895) : 3.66, 50.94% ; on skin.

PEROMYSCUS LEUCOPUS LEUCOPUS (Rafinesque)

PROTOZOA

1. *Giardia microti* (Kofoid and Christiansen 1915) : 100% ; intestine.

TREMATODA

2. *Entosiphonus thompsoni* (Sinitzin 1931) : 0.11, 3.7% ; jejunum.

NEMATODA

3. Larval nematodes : 0.11, 1.85% ; encysted in the wall of the caecum.
4. *Rictularia coloradensis* (Hall 1916) : 0.203, 16.68% ; duodenum and jejunum.
5. *Syphacia peromysci* n. sp. : 4.94, 22.22% ; caecum.

ARTHROPODA

DIPTERA

6. Larva of *Cuterebra fontinella* (Clark) : 0.037, 1.85% ; in skin.

MUS MUSCULUS MUSCULUS Linnaeus

PROTOZOA

1. *Endamoeba muris* (Grassi 1879) : 13.09% ; small intestine.
2. *Trichomonas muris* (Grassi 1879) : 30.95% ; caecum.

CESTODA

3. Larval stage of *Taenia taeniaeformis* (Batsch 1786) : 0.35, 3.57 ; liver.
4. *Hymenolepis diminuta* (Rudolphi 1819) : 0.14, 1.19% ; small intestine.

NEMATODA

5. *Heterakis spumosa* (Schneider 1866) : 0.97, 10.71% ; caecum and rectum.

ARTHROPODA

ACARINA

6. *Echinolaelaps echidninus* (Berlese) : 0.04, 1.19% ; on skin.

SIPHONAPTERA

7. *Xenopsylla cheopis* (Rothschild 1903) : 0.15, 10.51% ; on skin.

RATTUS NORVEGICUS (Erxleben)

PROTOZOA

1. *Chilomastix bettencourti* (Fonseca 1913) : 5.4% ; intestine.
2. *Endamoeba muris* (Grassi 1879) : 1.8% ; small intestine.
3. *Trichomonas muris* (Grassi 1879) : 60% ; caecum.
4. *Trypanosoma lewisi* (Kent 1880) : 1.8% ; blood.

CESTODA

5. Larval stage of *Taenia taeniaeformis* (Batsch 1786) : 0.36, 12.72% ; liver.
6. *Hymenolepis diminuta* (Rudolphi 1819) : 0.29, 7.27% ; jejunum.

NEMATODA

7. Eggs of *Capillaria hepatica* (Bancroft 1893) : 2.6% ; liver.
8. *Heterakis spumosa* (Schneider 1866) : 0.52, 14.54% ; caecum and rectum.
9. *Nippostrongylus muris* (Yokogawa 1920) : 102.76, 78.18% ; duodenum and jejunum.
10. *Trichosomoides crassicauda* (Bellingham 1845) : 1.3, 47.2% ; urinary bladder.

ARTHROPODA

ACARINA

11. *Echinolaelaps echidninus* (Berlese) : 4.14, 27.27% ; on skin.

ANOPLURA

12. *Polyplax spinulosa* (Burmeister 1839) : 1.98, 7.27% ; on skin.

SIPHONAPTERA

13. *Xenopsylla cheopis* (Rothschild 1903) : 0.018, 1.8%.

The following parasites infested seven rats examined at Beaufort, N. C.

CESTODA

1. *Hymenolepis diminuta* (Rudolphi 1819) : 5.57, 71.42% ; jejunum.
2. *Hymenolepis nana* (Siebold 1852) : 3.85, 14.28% ; jejunum.
3. Larval stage of *Taenia taeniaeformis* (Batsch 1786) : 0.14, 14.28% ; liver.

NEMATODA

4. *Heterakis spumosa* (Schneider 1866) : 16.14, 85.71% ; caecum and rectum.
5. *Nippostrongylus muris* (Yokogawa 1920) : 28, 85.71% ; duodenum and jejunum.
6. *Trichosomoides crassicauda* (Bellingham 1845) : 4, 71.42% ; urinary bladder.

ARTHROPODA

ACARINA

7. *Echinolaclaps echidninus* (Berlese) : 3.42, 57.14% ; on skin.

SIPHONAPTERA

8. *Echidnophaga gallinacea* (Westwood 1875) : 1.14, 14.28% ; on skin.
9. *Xenopsylla cheopis* (Rothschild 1903) : 3.42, 57.14% ; on skin.

SYLVILAGUS FLORIDANUS MALLURUS (Thomas)

PROTOZOA

1. *Eimeria stiedae* (Lindemann 1865) : 36.58% ; white cysts in the liver.
2. *Enteromonas intestinalis* (Fonseca 1918) : 75.6% ; caecum.

TREMATODA

3. *Hasstilcsia tricolor* (Stiles and Hassall 1894) : 1903.6, 41.46% ; small intestine.

CESTODA

4. Immature *Cittotaenia pectinata* (Goeze 1782) : 7.48, 78.07% ; duodenum and jejunum.
5. Mature *Cittotaenia pectinata* (Goeze 1782) : 1.78, 78.07% ; jejunum.
6. Larval stage of *Taenia pisiformis* (Bloch 1780) : 1.8, 31.7% ; attached to peritoneum or abdominal mesenteries.

NEMATODA

7. *Obeliscoides cuniculi* (Graybill 1923) : 19.63, 70.73% ; attached to the gastric mucosa.
8. *Trichostrongylus affinis* (Graybill 1924) : 48.14, 58.53% ; caecum and colon.
9. *Trichostrongylus calcaratus* (Ransom 1911) : 207.21, 80.48% ; duodenum and jejunum.

ARTHROPODA

ACARINA

10. *Haemaphysalis leporis-palustris* (Packard 1869) : 51.02, 100% ; on skin.
Larvae : 12.9, 36.58%.
Nymphs : 10.6, 48.78%.
Adults : 27.4, 100%.

SIPHONAPTERA

11. *Cediopsylla simplex* (Baker 1895) : 7.7, 78.04% ; on skin.
12. *Odontopsyllus multispinosus* (Baker 1904) : 1.26, 17.97% ; on skin.

DIPTERA

13. Larva of *Cuterebra fontinella* (Clark) : 0.12, 7.07% ; in skin.

SUMMARY OF FINDINGS

PROTOZOA

There is a fundamental difference between protozoan infestations and helminthic infestations in that the protozoan parasites multiply in the body, resulting in a fluctuation in numbers, whereas in helminthic infestations the organisms do not multiply in the body and can be increased in number only by repeated reinfestation (Chandler, 1932).

Eight species of protozoa were found infesting the rodents examined by the writer. Squirrels were not regularly examined for protozoa but when examinations were made no protozoans were found. The white-footed mouse harbored one species; the house mouse, two species; the rat, four species; the rabbit, two species.

Giardia microti infested all of the white-footed mice examined by the writer. It was usually found in the duodenum but occasionally in the ileum and caecum.

Trichomonas muris was found infesting the caecum and occasionally the ileum of 60 per cent of the rats and in 30.95 per cent of the house mice examined by the writer. The presence of this protozoan is correlated with a pH of approximately 6.8 (Kofoid, McNeil, and Bonestell, 1933). The other protozoans found in rats were very rare. *Trypanosoma lewisi*, a blood protozoan, was found in one rat; *Chilomastix bettencourti*, in three rats; *Endamoeba muris* in one rat. The latter protozoan was more common in house mice, 13.05 per cent being infested.

Enteromonas intestinalis infested the caecum and colon of 75.6 per cent of the rabbits studied by the writer; *Eimeria stiedae* infested the liver of 36.58 per cent.

TREMATODES

Only two species of trematodes were found infesting the rodents examined by the writer. These parasites usually require a snail as an intermediate host and many species of trematodes are not expected in land animals in a region in which there is a paucity of fresh water.

Hasstilesia tricolor occasionally infested rabbits in enormous numbers at any season of the year. Seventeen (41.46 per cent) of the rabbits examined by the writer harbored this parasite, with an average of 1,903 parasites per host. The life history of this parasite is unknown but it probably encysts as the metacercaria upon vegetation. Infestation probably results from the ingestion of the encysted stage with the food. No correlation between the habitat of the host and the parasitic infestation can be made since the rabbit is a roaming animal.

Entosiphonus thompsoni, a trematode which is usually found in shrews, was found in two white-footed mice. The largest number of ENTOSIPHONUS

present in a single infestation was four. Krull (1934) also found this trematode in the same host. The life-history of this species is unknown.

CESTODES

Five species of tapeworms infested the rodents examined. No cestodes were found in *Peromyscus* and, with the exception of one instance where a host contained a larva of *Taenia taeniaeformis*, none was found in squirrels. Three species were found in rats or mice and two infested rabbits.

Hymenolepis diminuta, a common tapeworm of the rat, was encountered in only 7.27 per cent of the rats examined by the writer. This tapeworm requires an intermediate insect host and the ingestion of the latter by a rat for completion of its life cycle. Although only seven rats were examined at Beaufort, *H. diminuta* was found in five of them, with an average of 5.5 worms per host.

Hymenolepis nana, the dwarf tapeworm, was found in one rat examined at Beaufort, twenty-seven being present. This parasite infests rats and man in various parts of the world. It is unique among cestodes in that it is capable of completing its development from egg to adult in a single host.

The larval stage of *Taenia taeniaeformis*, the cat tapeworm, was found in 12.72 per cent of 35 rats and in 3.57 per cent of 84 house mice examined. The largest number of parasites in an individual infestation was seven found in a rat in February. This parasite occurred occasionally throughout the year in rats but it was never abundant (Table 4). The squirrel harbored a single

TABLE 1

Sciurus carolinensis carolinensis

Showing occurrence of parasites during the months from September to May. The upper figures in each instance indicates average number of parasites per host; the lower, the percentage of hosts infested.

| | Sept. | Oct. | Nov. | Dec. | Jan. | Feb. | Mar. | Apr. | May |
|----------------------------------|-----------------|--------------|---------------|--------------|--------------|---------------|--------------|--------------|-----------|
| Number of hosts examined | 7 | 10 | 8 | 5 | 10 | 6 | 3 | 3 | 1 |
| <i>Taenia taeniaeformis</i> | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0.16 16.66 | 0 0 | 0 0 | 0 0 |
| <i>Longistriata hassalli</i> | 110.33 95.71 | 102.6 100 | 101 87.77 | 13 60 | 106.9 100 | 62.33 100 | 19.33 100 | 46 100 | 16 100 |
| <i>Trombicula</i> sp. | 7.0 42.75 | 14.1 60 | 14.75 87.5 | 1.8 60 | 1.3 50 | 0.33 16.66 | 2.0 66.66 | 0 0 | 0 0 |
| <i>Atricholaelaps glasgowi</i> | 0.57 28.57 | 0.1 10 | 0 0 | 0 0 | 0.9 30 | 0 0 | 1 30 | 0 0 | 0 0 |
| <i>Ixodes hexagonus</i> | 0.14 14.2 | 0.2 10 | 0 0 | 0.2 20 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Neohaematopinus sciurinus</i> | 2.7 14.44 | 2.6 50.0 | 6.5 87.5 | 80.2 100 | 101.3 90 | 2.16 16.66 | 0 0 | 0 0 | 0 0 |
| <i>Hoplopleura sciuricola</i> | 0.7 14.44 | 0 0 | 0.25 12.5 | 2.2 60.0 | 17.8 70.0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Orchopeas wickhami</i> | 0.72 28.57 | 0.3 20.0 | 1.0 62.5 | 13.6 60.0 | 3.1 60.0 | 9.5 66.66 | 7.0 100 | 1.33 33.3 | 1 100 |

TABLE 3
Mus musculus musculus

Showing occurrence of parasites during the months of the year, June, 1934 to April, 1935. The upper figure in each instance indicates average number of parasites per host; the lower the percentage of hosts infested.

| | Jan. | Feb. | Mar. | June | July | Aug. | Oct. | Nov. | Dec. |
|-------------------------------------|---------------|-----------|---------|--------------|--------------|--------------|-------------|-------------|--------------|
| Number of hosts examined | 7 | 8 | 5 | 7 | 16 | 33 | 5 | 7 | 6 |
| <i>Endamoeba muris</i> | 0 0 | 0 0 | 0 0 | 71.4 0 | 18.7 6.2 | 13.04 8.6 | 0 0 | 0 0 | 0 0 |
| <i>Trichomonas muris</i> | 57.42 0 | 50.0 0 | 40 0 | 28.5 0 | 43.7 0 | 13.04 0 | 20.0 0 | 42.8 0 | 33.3 0 |
| <i>Taenia taeniaeformis</i> (larva) | 0 0 | 0 0 | 0 0 | 0 0 | 0.06 6.2 | 0.08 8.6 | 0 0 | 0 0 | 0 0 |
| <i>Hymenolepis diminuta</i> | 0 0 | 0 0 | 0 0 | 1.71 14.2 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Heterakis spumosa</i> | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0.95 4.3 | 1.4 20.0 | 7.0 85.7 | 0.16 16.6 |
| <i>Echinolaelaps echidninus</i> | 0.57 14.28 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Xenopsylla cheopis</i> | 0 0 | 0 0 | 0 0 | 0 0 | 0.43 31.2 | 0.26 17.3 | 0 0 | 0 0 | 0 0 |

house mice, the same oxyuroid as rats. All of the nematodes with the exception of *Trichosomoides crassicauda* infested the digestive system. The heligmosomid, *Longistriata hassalli*, was found in 92.45 per cent of the 53 squirrels examined, with an average of 77.5 per host. Table 1 shows this species to be very common throughout the period of study. No information concerning seasonal variation was obtained since no squirrels were examined during the summer months, but the worm probably is present throughout the year. The small number of parasites found in some of the hosts was influenced by the age of the host as young animals were usually not infested. Infestation by *Longistriata hassalli* is probably by skin penetration, the common method of infestation of other heligmosomids.

Rictularia coloradensis, a spiruroid, was encountered in 16.66 per cent of 54 white-footed mice examined by the writer. It usually occurred singly but occasionally two females were present. The males of RICTULARIA apparently do not remain long in the host, as none was found. Table 2 shows that no parasites were found during the first four months of the year. No examinations were made in May. The life-history of RICTULARIA is unknown.

Syphacia peromysci, n. sp., the oxyuroid of PEROMYSCUS, was found living free in the caecum. It was present in 22.22 per cent of the white-footed mice examined, with an average of 4.94 per host. It appears occasionally throughout the year (Table 2). The life-history of this species is unknown but probably simple as in other oxyuroids.

Heterakis spumosa, a rat and mouse nematode, is a non-pathogenic oxyuroid inhabiting the caecum and colon of rats and mice. It is rather

TABLE 4
Rattus norvegicus

Showing occurrence of parasites during the months of the year, May, 1934 to April, 1935. The upper figures in each instance indicates average number of parasites per host; the lower the percentage of hosts infested.

| | Jan. | Feb. | Mar. | May | June | July | Aug. | Oct. | Nov. | Dec. |
|-------------------------------------|----------------|---------------|---------------|--------------|---------------|---------------|-----------------|----------------|---------------|--------------|
| Number of hosts examined.... | 6 | 5 | 7 | 5 | 5 | 5 | 4 | 8 | 5 | 4 |
| <i>Chilomastix bettencourti</i> | 0 0 | 0 0 | 0 0 | 20 40 | 40 20 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Endamoeba muris</i> | 0 0 | 0 0 | 0 0 | 0 20 | 20 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Trichomonas muris</i> | 50 16.6 | 60 0 | 66.66 0 | 80 0 | 60 0 | 60 0 | 75 0 | 62.5 0 | 60 0 | 50 0 |
| <i>Trypanosoma lewisi</i> | 16.6 0 | 0 40.0 | 0 14.25 | 0 20.0 | 0 20.0 | 0 0 | 0 0 | 0 25.0 | 0 0 | 0 0 |
| <i>Taenia taeniaeformis</i> (larva) | 0 0 | 1.8 40.0 | 0.14 14.25 | 0.4 20.0 | 1 20.0 | 0 0 | 0 0 | 0.37 25.0 | 0 0 | 0 0 |
| <i>Hymenolepis diminuta</i> | 0.16 16.66 | 0 0 | 0 0 | 0 0 | 0 0 | 2.8 40.0 | 0.25 25.0 | 0 0 | 0 0 | 0 0 |
| <i>Capillaria hepatica</i> (eggs) | 0 0 | 0 0 | 14.2 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 20 0 |
| <i>Heterakis spumosa</i> | 0.16 16.0 | 0 0 | 0 0 | 2.8 20.0 | 2.4 40.0 | 0.4 40.0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Nippostrongylus muris</i> | 122.83 83.3 | 44.6 100.0 | 71.57 62.5 | 6.2 40.0 | 146.4 80.0 | 71.4 100.0 | 208.25 100.0 | 247.37 87.5 | 39.2 80.0 | 17.5 25.0 |
| <i>Trichosomoides crassicauda</i> | 2.16 83.33 | 1.0 40.0 | 1.57 57.14 | 1.8 40.0 | 1.2 40.0 | 1.0 40.0 | 1.0 25.0 | 1.62 37.5 | 1.0 40.0 | 0.75 40.0 |
| <i>Echinolaclaps echidninus</i> | 7.16 50.0 | 1.2 60.0 | 7.57 28.57 | 9.2 40.0 | 0 0 | 0 0 | 0 0 | 0.36 12.5 | 12.83 33.3 | 0 0 |
| <i>Polyplax spinulosa</i> | 0 0 | 0 0 | 0.57 14.2 | 20.6 40.0 | 0 0 | 0 0 | 0 0 | 0.12 12.0 | 0 0 | 0 0 |
| <i>Xenopsylla cheopis</i> | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0.25 25.0 |

common in other parts of the United States. It was rarely encountered during this survey. Eight of the 55 rats examined by the writer harbored these parasites, which were present during the summer months with the exception of a single individual found in January (Table 4). The eggs of *Heterakis spumosa* are viable for long periods of time under favorable conditions of temperature and moisture. They develop rapidly at summer temperatures. The life history is simple and the eggs become infective within fourteen days (Winfield, 1932). The mice on the other hand, harbored this parasite during the winter months (Table 3). The highest single infestation was 17 worms in a mouse examined in November when six of seven mice were infested. In general the rats of Beaufort appear to be more highly infested with this parasite than are those in Durham. Four of the seven rats examined showed comparatively high infestations—46, 29, 21 and 14 respectively.

The rat strongyloid, *Nippostrongylus muris*, was found in 78.18 per cent of the 55 rats examined by the writer. Large numbers were found in individual rats giving an average of 247.3 worms per host. The largest number

of worms found in an individual rat was 951. The infective larvae of *N. muris* enter rats by boring through the skin. When they are fed to rats only a small proportion are able to reach the intestine (Yokogawa, 1922). The infective larvae are carried to the lungs by the blood stream and pass through the respiratory system to the digestive system by way of the trachea.

The trichuroid, *Trichosomoides crassicauda*, is a parasite of the urinary tract of rats. It occurred in 47.2 per cent of the 55 rats studied by the writer, with an average of 1.3 worms per host. The parasites were present at any season of the year (Table 4). The largest number of worms present in a single infestation was 7. Infestation with this worm is by the ingestion of the eggs. The larvae are dispersed by means of the blood stream. Only those larvae which reach the urinary tract in their wanderings after having left the blood stream reach sexual maturity (Thomas, 1922).

TABLE 5

Sylvilagus floridanus mallurus

Showing occurrence of parasites during all months of the year, October, 1933 to September, 1934. The upper figures in each instance indicates average number of parasites per host; the lower, the percentage of hosts infested.

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Oct. | Nov. | Dec. |
|--|----------------|----------------|----------------|----------------|----------------|----------------|---------------|---------------|---------------|---------------|---------------|
| No. of hosts examined | 5 | 5 | 3 | 3 | 2 | 4 | 3 | 3 | 4 | 6 | 4 |
| <i>Eimeria stiedae</i> | 20 20 | 60 60 | 33.3 33.3 | 66.6 66.6 | 0 0 | 50 50 | 33.3 33.3 | 66.6 66.6 | 25.0 25.0 | 0 0 | 50.0 50.0 |
| <i>Enteromonas intestinalis</i> | 60 60 | 80 80 | 100 100 | 66.6 66.6 | 100 100 | 100 100 | 66.6 66.6 | 66.6 66.6 | 75.0 75.0 | 66.6 66.6 | 50.0 50.0 |
| <i>Haustorium tricolor</i> | 5152.2 80.0 | 2200.0 20.0 | 183.3 33.3 | 5696.0 66.6 | 0 0 | 5043.7 50.0 | 694.6 66.6 | 166.6 33.3 | 0 0 | 143.0 16.6 | 40.25 75.0 |
| <i>Cittotaenia pectinata</i> Mature | 1.2 80.0 | 1.4 80.0 | 1.0 66.6 | 0.66 33.3 | 3.0 100 | 3.25 75.0 | 1.66 66.6 | 1.66 66.6 | 3 75 | 1.0 83.3 | 1.75 100 |
| <i>C. pectinata</i> Immature | 6.4 60.0 | 9 40 | 3 66.6 | 3.6 100 | 50 100 | 7.8 100 | 8 66.6 | 1.33 66.6 | 3.0 25.0 | 1.16 33.3 | 3 75 |
| <i>Taenia pisiformis</i> (larva) | 1.6 40.0 | 0 0 | 2.66 66.6 | 2.33 33.3 | 3.5 50.0 | 6.25 50.0 | 0.33 33.3 | 0.33 33.3 | 3.75 50.0 | 0.5 16.6 | 0 0 |
| <i>Obeliscoides cuniculi</i> | 6.8 20.0 | 38.6 60.0 | 24.66 100.0 | 36.3 100.0 | 12.0 100.0 | 28.25 100.0 | 28.0 100.0 | 2.66 66.6 | 12.3 66.6 | 18.0 66.6 | 5.75 50.0 |
| <i>Trichostrongylus affinis</i> | 0 0 | 29.4 40.0 | 8.0 66.6 | 267.3 100.0 | 69.5 100.0 | 109.2 100.0 | 92.3 100.0 | 19.0 66.6 | 3.75 50.0 | 10.1 33.3 | 3.75 50.0 |
| <i>T. calcaratus</i> | 71.8 60.0 | 132.2 80.0 | 290.6 100.0 | 910.0 100.0 | 403.5 100.0 | 495.7 100.0 | 173.3 66.6 | 21.6 66.6 | 49.3 50.0 | 37.3 66.6 | 26.7 100.0 |
| <i>Haemaphysalis leporis-palustris</i> * | 4.8 80.0 | 2.2 40.0 | 4.0 100.0 | 15.0 100.0 | 0 0 | 0 0 | 10.0 66.6 | 4.3 33.3 | 54.0 75.0 | 26.1 66.6 | 9.0 100.0 |
| nymphs | 4.4 80.0 | 1.6 40.0 | 6.6 66.6 | 7.0 100.0 | 48.5 100.0 | 5.5 50.0 | 5.3 66.6 | 16.6 100.0 | 31.5 75.0 | 5.6 50.0 | 4.75 75.0 |
| adults | 20.8 100.0 | 9.4 100.0 | 30.6 100.0 | 68.6 100.0 | 113.0 100.0 | 53.0 100.0 | 18.6 100.0 | 60.6 100.0 | 42.0 100.0 | 3.0 100.0 | 6.25 100.0 |
| <i>Cediopsylla simplex</i> | 5.2 80.0 | 12.1 100.0 | 28.6 100.0 | 13.6 100.0 | 4.5 100.0 | 9.7 100.0 | 1.5 50.0 | 4.0 66.6 | 0 0 | 2.8 66.6 | 2.2 75.0 |
| <i>Odontopsyllus multispinosus</i> | 0.2 20.0 | 0.6 20.0 | 12.6 100.0 | 3.3 66.6 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| <i>Cuterebra fontinella</i> * | 0.2 20.0 | 0 0 | 0 0 | 0 0 | 0 0 | 0.25 25.0 | 0 0 | 0 0 | 0.75 50.0 | 0 0 | 0 0 |

*Larvae

The trichuroid, *Capillaria hepatica*, was represented only by eggs in the liver of two rats. Infestation by this nematode is brought about by the ingestion of the eggs. Transmission is presumably through the eating of dead infested rats. If mature eggs are ingested hatching takes place in the small intestine and the newly liberated larvae, after penetrating the intestinal wall, reach the liver by way of the circulatory system according to Fülleborn (1924), but Nishigori (1925) and Asada (1925) believe that larvae pass through the intestinal wall into the abdominal cavity and then penetrate into the liver.

Only one specimen of the spiruroid, *Protospirura muris*, was found. This parasite requires an intermediate host such as a cockroach (Cram, 1926) during its life cycle.

The rabbit stomach worm, *Obeliscoides cuniculi*, was found in 70.73 per cent of the 41 rabbits examined by the writer, with an average of 19.6 per host. Examination of stomach walls of infested rabbits usually showed congestion of the gastric mucosa with numerous hemorrhages. The worms were usually free on the mucous membrane or embedded deep in the stomach wall. The rabbits examined by the writer show that infestation of *OBELISCOIDES* may occur throughout the year (Table 5). The largest number of worms found in an individual rabbit was 166. Infestation takes place through the mouth. There is no penetration of the skin by the infective larvae (Alicata, 1932).

The duodenum-jejunum nematode, *Trichostrongylus calcaratus*, occurred in 80.48 per cent of the rabbits examined by the writer, with an average of 207.2 per host. *Trichostrongylus affinis*, a nematode inhabiting the caecum and colon, was found in 58.53 per cent of the hosts examined, with an average of 48.1 per cent per host. Infestation of rabbits by species of *TRICHOSTRONGYLUS* may take place either through the skin or with the food. The latter is the more common mode of infestation (Sarles, 1932).

ARTHROPODS

Thirteen species of arthropods were found infesting the rodents studied by the writer. Squirrels carried six species; house mice, two species; rats, three species; rabbits, four species. No arthropods were found on *PEROMYSCUS*, which were caught in snap traps, with the exception of two larvae of *Cuterebra fontinella* infesting one host.

Of the two mites found infesting the squirrels examined by the writer, an unidentified species of *TROMBICULA* larva, a chigger mite, was more common. It was found on 50.94 per cent of the 53 squirrels examined with an average of 6.35 per squirrel. The largest number of *TROMBICULA* found upon an individual squirrel was 103. This larval mite, the adults of which are free living, occurred during seven of the eight months of squirrel examination.

None were found in April when only three squirrels were examined for parasites. The largest average number of mites was found in October and November (Table 1). Undoubtedly these mites would prove to be more numerous during the summer months when *Trombicula* larvae are very numerous.

The mite, *Atricholaelaps glasgowi*, and the tick, *Ixodes hexagonus*, were uncommon, the former infesting only seven squirrels with an average of 0.32 per host; the latter, four specimens from three squirrels.

The louse, *Neohaematopinus sciurinus sciurinus*, was found upon 50.94 per cent of the squirrels, with an average of 26.7 per host. This louse was most prevalent during the month of December when an average number of 80.2 per host occurred. Lice were found whenever there was an appreciable number of hosts examined. *Hoplopleura sciuricola* showed an infestation of 22.64 per cent with an average of 3.81 per host. The largest number of *HOPLOPLEURA* found in a single infestation was 129 on a squirrel examined during January.

The flea, *Orchopeas wickhami*, occurred on 50.94 per cent of the squirrels examined, with an average of 3.66 per host. The largest number of fleas found was 57, found on a squirrel examined in December. Fleas were not prevalent during any of the months of the survey.

The rats examined by the writer harbored a mite, *Echinolaelaps echidninus*, a louse, *Polyplax spinulosa* and the tropical rat flea, *Xenopsylla cheopis*.

The mite was the most common, occurring on 27.27 per cent of the 55 rats examined, with an average of 14.14 per host. No mites were found during the summer months. The average number of parasites per monthly number of rats varied very little during the months it was present (Table 4).

The common rat louse was rarely collected (Table 4). Only 7.27 per cent of the rats were infested. The largest number of lice found was 53 in May. The average number per host was 1.98. Only one specimen of the tropical rat flea was collected. Fourteen *Xenopsylla cheopis* were collected from the 83 house mice examined. They were present only during July and August (Table 3). Low temperatures are harmful to the tropical rat flea (Bacot, 1914). The common rat flea, *Nosopsyllus fasciatus*, was not encountered during this survey. It appears that fleas are uncommon on Durham rats and mice. However at Beaufort, North Carolina, four of the six rats examined harbored fleas: *Xenopsylla cheopis* and *Echidnophaga gallinacea*, the tropical stick-tight flea. The average number of fleas per host was 3.42 for *Xenopsylla cheopis* and 1.14 for *Echidnophaga gallinacea*.

Two species of fleas and one species of tick were found infesting rabbits. *Haemaphysalis leporis-palustris*, the rabbit tick, was found upon all of the rabbits examined by the writer. This parasite requires three hosts upon which to feed in the larval, nymphal, and adult stages respectively. The

adults feed longer than the larvae or nymphs, therefore were found to be more numerous (Table 6).

Two species of fleas, *Cediopsylla simplex* and *Odontopsyllus multispinosus*. The former is the common rabbit flea of the Eastern United States and was found throughout the year. *Odontopsyllus multispinosus* is rather uncommon and was found only from February to May (Table 5). The greatest number occurred in March, an average of 12.6 per host. *Cediopsylla simplex* was more prevalent during February, March, and April (Table 5).

Four rabbits harbored the larval stages of a fly, *Cuterebra fontinella* (Table 5).

DISCUSSION

The preceding summary indicates that there is a predominance of internal parasites in the rabbits and rats, which are of larger size than the other rodents studied and therefore offer a more suitable habitat for parasites. Both are voracious feeders and thus permit greater infestation. Numerous rabbits and rats facilitate the dispersal of the parasites through faeces, thus enhancing the opportunity for infestation and reinfestation. A rat is omnivorous and has filthy habits which make infestation easy through the ingestion of eggs or larvae or by skin penetration. Pearse (1930) found that large, omnivorous, cursorial rodents usually are the most highly parasitized. The prevalence of *Hymenolepis diminuta*, which requires an intermediate host for completion of its life history, at Beaufort is probably due to the comparatively large number of fleas infesting the rats. The rats of Durham are not very heavily infested with fleas and show little infestation with this tapeworm (Table 4). Pearse (1930) states that mature tapeworms are common in mammals in open fields. The writer has observed a dominance of tapeworms in the rabbit, which lives in the field and forest.

The squirrel, although a comparatively large rodent, was infested with only one species of internal parasite, a strongyloid nematode. It is a comparatively clean arboreal animal. Its food is usually limited to fruits, nuts, seeds, buds and bark, thus apparently limiting infestation by parasites. The infestation by the single nematode undoubtedly takes place during short forays upon the ground. The squirrels showed high infestation of this nematode (Table 1) "probably because shade and moisture in forests are favorable for the development of the eggs and because when the hosts visit the ground they go again and again to situations which are favorable for infestation" (Pearse, 1930).

Small rodents such as house mice and Peromysci do not offer very favorable habitats for any large number of parasites. It is a recognized fact that small animals usually harbor few parasites. The parasites which occur in great numbers must necessarily be minute in size.

Squirrels carried more species of external parasites than any other rodent studied by the writer (Table 1). Squirrels have a permanent nest to which they return. They run about on the ground and may become infested in this way. However, infestation is easier in the nest which is suitable for breeding and metamorphosis of the parasites. Lice and *TROMBICULA* larvae showed specificity for squirrels and were only common on them. Lice were occasionally collected from rats. Adult mites were found on rats although they were uncommon. The rabbit apparently is an ideal host for a large number of ticks. It is of a comparatively large size and frequents shrubby areas which favors tick infestation (Pearse, 1930).

SEASONAL VARIATION

No seasonal variation was demonstrated in *SCIURUS* since no examinations of squirrels were made during the summer months. Seasonal variation is evident only in the parasites of the rats and rabbits. These were numerous and occurred throughout the year thus giving opportunity for comparison of the degrees of infestation. No seasonal variation for *Hasstilesia tricolor*, *Hymenolepis diminuta*, larval tapeworms, *Trichosomoides crassicauda* and *Heterakis spumosa* was demonstrated.

Figure 1 shows a dominance of *CITTOTAENIA* during the spring and summer months. High initial infestation was followed by a decrease in numbers. In Canada rabbits are said to develop an almost complete immunity to *CITTO-TAENIA* with a change in diet from green vegetation to bark during the winter (Boughton, 1932). There is apparently a similar reaction in the rabbits studied by the writer. As the cestodes grow some of them are lost until only one or two adult parasites remain during the winter months.

Figures 2 and 3 indicate an increase of *Trichostrongylus affinis* and *T. calcaratus* during the spring months, with a gradual decrease in the number of worms later. The high infestation apparently is followed by a host immunity response with the discharge of worms (Stoll, 1932). As many as 2,000 *T. calcaratus* were taken from individual rabbits by the writer. In laboratory animals a lethal dose is approximately 1,000 worms (Sarles, 1932a). The results obtained by the writer indicate that there is a host immunity response similar to that found by Stoll (1932) and Sarles (1932) after experimental infestations. The decrease in the number of worms during the winter months is undoubtedly influenced by the unfavorable lower temperature for the free-living larval stages (Stoll, 1932).

Variations in temperature apparently influenced the seasonal variation of *Obeliscoides cuniculi* and *Nippostrongylus muris* (Tables 4 and 5). No evidences of immunity reactions to these parasites have been demonstrated. The immunity reactions of white rats to *Nippostrongylus muris* (Yokogawa, 1922) apparently does not hold true for the brown rat (Chandler, 1931).

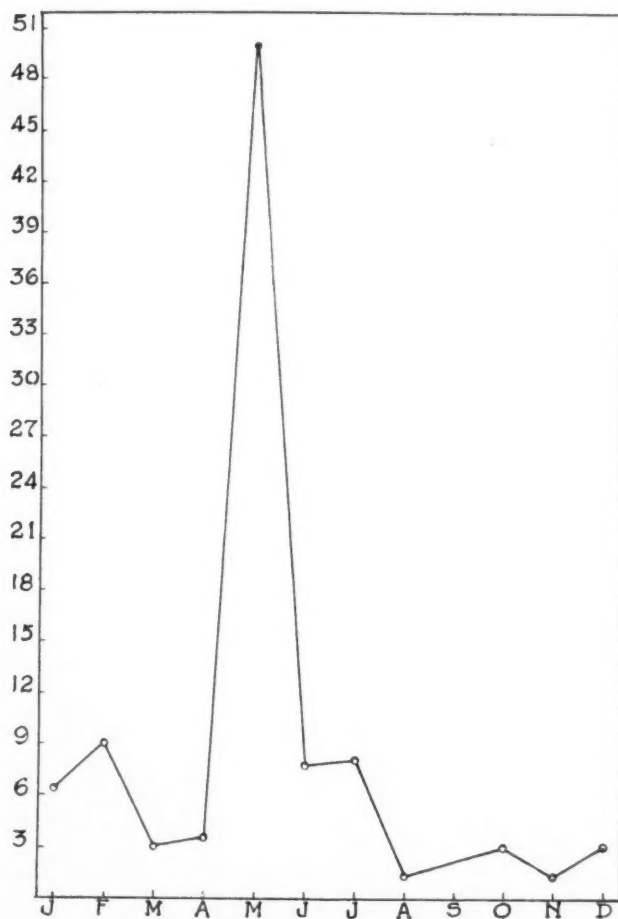


FIG. 1. Monthly variation in the average number of immature tapeworm, *Cittotaenia pectinata*, found in the cottontail rabbit, *Sylvilagus floridanus mollurus*, during a year.

Haemaphysalis leporis-palustris showed variations in the number of larvae, nymphs and adults appearing on the rabbits studied by the writer. The adults feed longer than the larvae or nymphs, therefore were found to be more numerous (Fig. 4). Hooker (1912) states from personal observation that large numbers of larvae and lesser numbers of nymphs when repleted abandon the host during the daytime. He regards this as an adaptation of the tick to the habits of their natural hosts, the hare and the rabbit. These remain during the day in their resting places and roam at night. The engorged ticks, dropping from the hosts in the resting places, undergo metamorphosis in a situation which favors their finding a host when they emerge and are ready to feed. In general the number of nymphs collected by the writer was greater than the number of larvae. The rabbits studied were collected during the day.

In Figure 4 an attempt is made to show the general succession of the

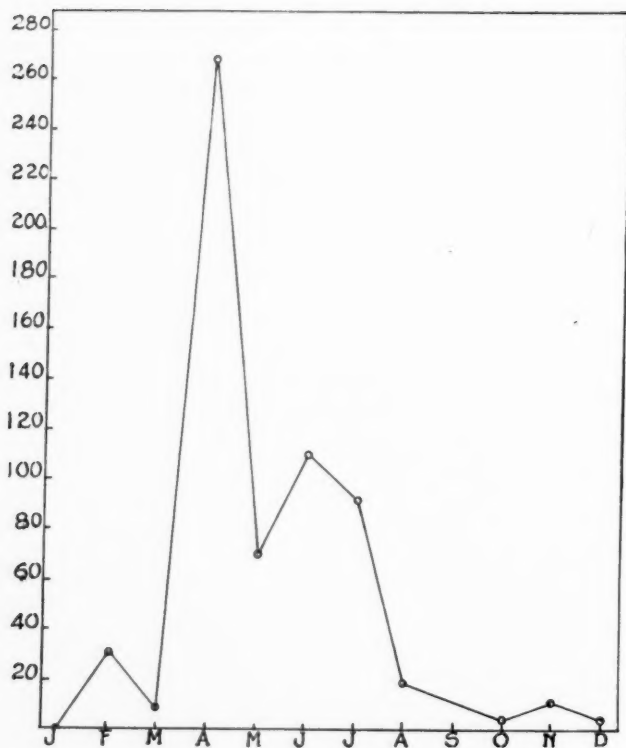


FIG. 2. Monthly variation in the average number of caecum nematode, *Trichostrongylus affinis*, found in the cottontail rabbit, *Sylvilagus floridanus malurus*, during a year.

various stages of *HAEMAPHYSALIS*. The larvae are comparatively numerous during April, July and October, approximately 90 days separating each successive increase. The time required for the life-history of this tick at summer temperature is 87 days (Nuttall, Warburton, Cooper, and Robertson, 1915). The nymphs show periods of increase in numbers during May, August, and October. The periods of nymphal predominance follow those of the larvae, demonstrating a correlation between infestation and the life-history. There are also variations in the number of adults infesting the rabbits but there is no definite correlation between infestation and life-history since the feeding time for the host is greater than that of the larvae or nymphs. In general the adults are most abundant during the spring and late summer. The rate of metamorphosis is dependent upon the temperature. Figure 4 shows the correlation between monthly mean temperature and the average number of larvae, nymphs and adults. There is a decrease in the number of ticks with a decrease in temperature. A greater amount of time is necessary for metamorphosis at low temperatures and thus there are fewer parasites infesting the host. *Haemaphysalis leporis-palustris* apparently completes its life-history twice during the year.

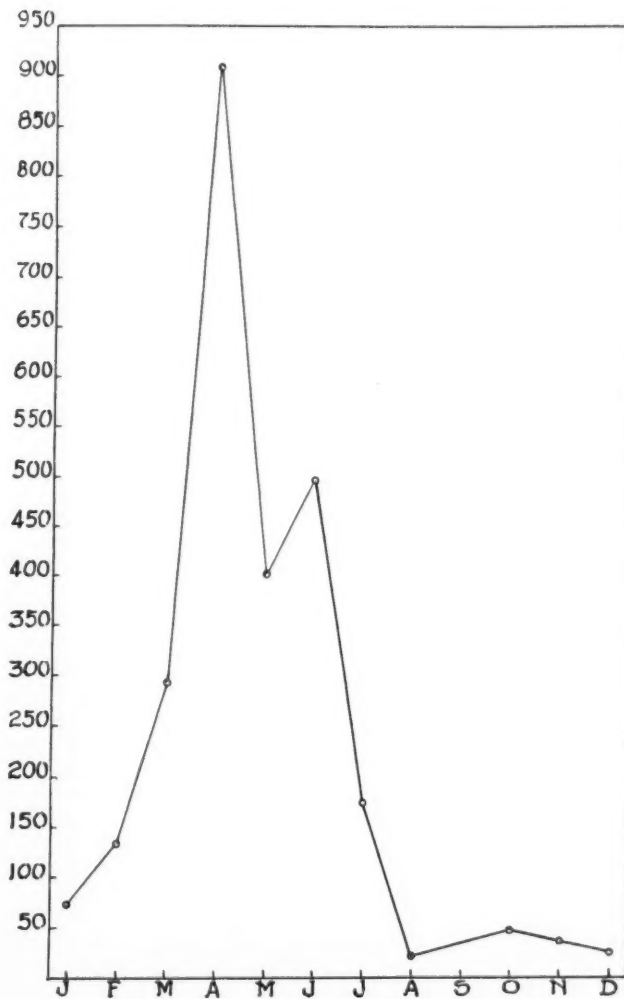


FIG. 3. Monthly variation in the average number of duodenum nematode, *Trichostrongylus calcaratus*, found in the cottontail rabbit, *Sylvilagus floridanus mollurus*, during a year.

Table 5 shows the prevalence of *Cediopsylla simplex* and *Odontopsyllus multispinosus* during February, March and April. Many fleas, e.g. *Nosopsyllus fasciatus* increase in numbers during the colder parts of the year (Bacot, 1914). This apparently holds true for *CEDIOPSYLLA* and *ODONTOPSYLLUS*. Furthermore, rabbits remain in their resting places for longer periods of time when the temperature is low, thus permitting easier infestation by fleas.

CONCLUSIONS

Nearly all evidence indicates the desirability of elimination from valuable agricultural, range, and forest areas, of such species as the prairie dog, ground squirrel, and rabbit. The pocket gopher in a citrus orchard or an alfalfa field

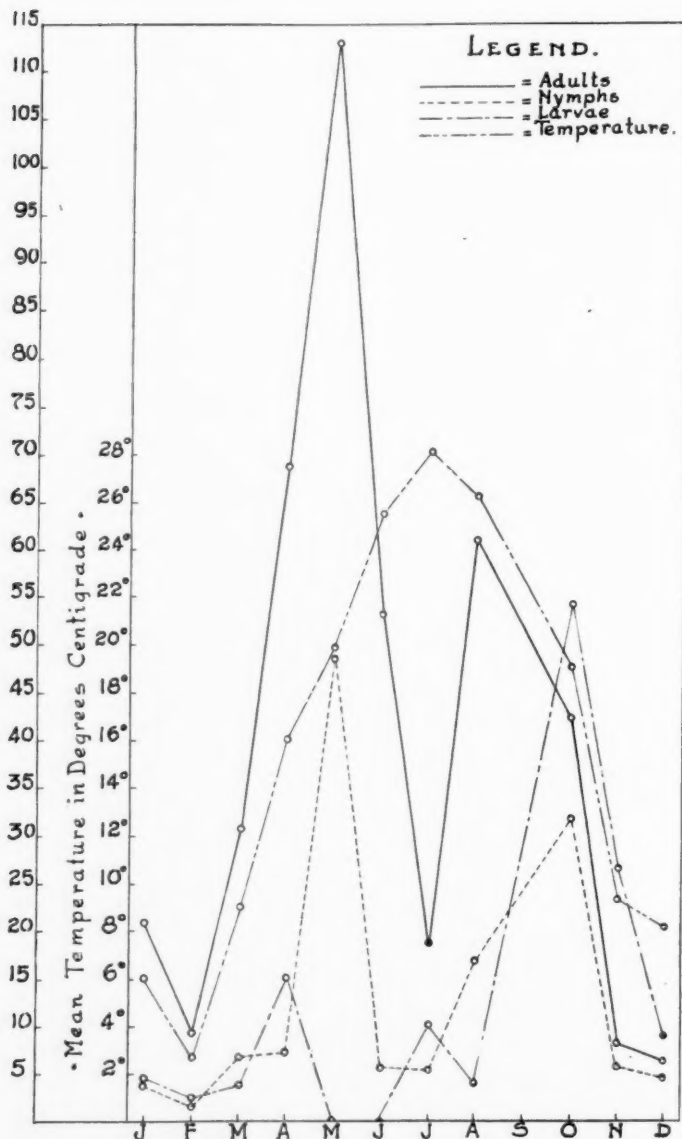


FIG. 4. Monthly variations in the average number of adults, nymphs, and larvae of the rabbit tick, *Haemaphysalis leporis-palustris*, during a year. The mean atmospheric temperature for the months in which observations were made is given.

is likewise undesirable. The California and Columbian ground squirrels must often be eliminated before profits can be made in cultivated areas. On the other hand, many rodents act as checks on insects. Some of the beneficial activities of rodents in the soil are: stirring up surface layers, increasing porosity; decreasing the size of particles; increasing aeration; increasing water percolation; helping to incorporate into the soil larger quantities of organic matter; depositing faeces and urine; depositing dead bodies. It must

be remembered that the injurious rodent effects are direct and easily observable, while beneficial rodent work is usually indirect and difficult to appreciate. The transmission of diseases by rats, ground squirrels, and rabbits is a menace to public health and control measures should be made with such rodents. The wholesale elimination of rodents has never been advocated, except for the obnoxious rat. "It is advisable to interfere with nature as much as necessary, but as little as possible" (Taylor, 1930).

A study of the writer's "List of Parasites of Rodents" makes one doubt the conception that a particular parasite is limited to a single host species and a single host may harbor but one species of a particular general group. Becker (1933) maintains that a particular parasite will develop in any host which provides satisfactory environmental conditions and mode of entrance and further that, "host-specificity becomes interpretable in terms of known physiological phenomena, and does not require any special interpretation involving a peculiar quality which species (host or parasite) possess that is separate and apart from what is observable in individuals."

Trematodes are uncommon in land rodents but in such aquatic types as the muskrat and beaver they are common. Trematodes are usually present in those rodents whose habitat are either in or near bodies of water. It is significant to note that the rodents of North Carolina, examined by the writer, showed only two species of trematodes and only one of these in any abundance.

It is a pertinent fact that the cestodes of the family Anoplocephalidae are well represented among herbivorous mammals. *Cittotaenia pectinata*, only adult cestode found in rabbits, is a member of this family. The life histories of the members of this family are unknown. Douthitt (1915) maintains that the type of soil determines infestation by anoplocephalids.

Omnivorous or insectivorous rodents usually harbor species of tapeworms belonging to families other than Anoplocephalidae. *HYMENOLEPIS* is a parasite of rodents and birds. These hosts are insect eaters and the birds more so than the rodents. There is a greater representation of Hymenolepididae in birds than in rodents.

Susceptibility, food, size and habits of the host, soil, and temperature undoubtedly influence the type of parasite and the degree of infestation. Seasonal periodicity may be influenced to some extent by the age of the host. Within the past 10 years there has been a widespread interest in observations or experiments dealing with the subject of resistance and susceptibility of helminthic infestations. Resistance to infestation or reinfestation by internal parasites has been shown to be correlated to some extent with the physiological status of the host. Rabbits show a tendency to lose their worms after initial infestation. Some of them show positive resistance to certain nematodes and show no infestation with them (Stoll, 1932). Furthermore, the

tendency to lose parasites may be associated with parasitic over-crowding, in the case of large tapeworms. The intestinal flora, and pH, undoubtedly influence the appearance and disappearance of internal parasites. Rabbits tend to lose their parasites in the winter months when food is scarce and the hosts resort to a bark diet (Boughton, 1932). An arboreal animal with a restricted herbivorous diet, for example, the squirrel, shows fewer internal parasites than a terrestrial animal which is omnivorous or has a non-restricted herbivorous diet, for example, rat and rabbit. In general the number of species of parasites is directly proportional to the size of the host. Temperature probably to some degree controls the infestation of hosts by fleas and ticks. It may influence the varying degrees of internal parasites during the various seasons, low temperatures being unfavorable to the free-living larvae.

SUMMARY

1. Scientific rodent control is advisable.
2. Two hundred eighty-seven rodents were examined for parasites: 53 gray squirrels, 54 white-footed mice, 84 house mice, 55 brown rats and 41 cottontail rabbits.
3. Eight species of protozoa were found infesting the rodents examined: white-footed mouse, 1; house mouse, 2; rat, 4; rabbit, 2.
4. Trematodes were uncommon in the rodents studied. One species was found in the white-footed mouse and one in the rabbit.
5. The rat, house mouse and rabbit were the only rodents found to harbor adult cestodes.
6. Eleven species of nematodes were found: squirrel, 1; white-footed mouse, 2; rat and house mouse, 5; rabbit, 3.
7. Seventeen species of arthropods infested the rodents examined: squirrel, 6; white-footed mouse, 1; rat, 4; house mouse, 2; rabbit, 4.
8. Smaller rodents harbor fewer parasites than do larger hosts.
9. Rodents having permanent nests are parasitized with more species of external parasites than are other rodents.
10. Arboreal habit lessens the possibility of internal parasites.
11. The type of food influences the character and degree of parasitism. Insectivorous rodents harbor cestodes requiring an insect as intermediate host. Herbivorous rodents harbor species of Anoplocephalidae, the life-histories of which are unknown.
12. Seasonal periodicity of parasites is influenced by temperature and change of diet. Susceptibility of hosts and immunity responses probably influence periodicity of infestation.
13. A list of parasites of North American rodents is presented in Appendix I.

14. The description of a new species of nematode from the white-footed mouse is presented in Appendix II.

APPENDIX I

A LIST OF PARASITES OF RODENTS

Here are listed the parasites reported from North American Rodentia and Lagomorpha. The parasites are arranged alphabetically under appropriate systematic groups and the hosts are listed in alphabetical order under them. Localities and bibliographic references for hosts are given whenever possible.

PROTOZOA

Babesia citelli Becker and Roudabush 1934

Citellus tridecimlineatus t.; Iowa; Becker and Roudabush 1934, 524.

Balantidium sp.

Dasyprocta aguti; Strong, Shattuk and Wheeler 1926, 130.

Rattus norvegicus; Atchley 1935, 183.

Chilomastix bettencourti (Fonseca 1915)

Rattus norvegicus; United States; Kofoid, McNeil and Bonestell 1933, 187.

C. magna Becker 1926

Citellus tridecimlineatus texensis; Iowa; Becker 1926, 288.

Councilmania decumani Kofoid, Swezey and Kessel 1923

Rattus norvegicus; Cosmopolitan; Kofoid, McNeil and Bonestell 1933, 187.

Eimeria beecheyi Henry 1932

Otospermophilus grammurus g.; California; Henry 1932, 280.

E. bilamellata Henry 1932

Callospermophilus chrysodeirus c.; California; Henry 1932, 282.

E. callospermophili Henry 1932

Callospermophilus chrysodeirus c.; California; Henry 1932, 287.

E. citelli Kartchner and Becker 1930

Citellus tridecimlineatus t.; Iowa; Kartchner and Becker 1930, 20.

E. cuniculi (Revolta 1878)

Oryctolagus cuniculus domesticus; Levine and Becker 1933, 86.

E. cynomysis Andrews 1928

Cynomys ludovicianus l.; Levine and Becker 1933, 86.

E. eubeckeri Hall and Knipling 1935

Citellus franklinii; Iowa; Hall and Knipling 1935, 129.

E. falciformis (Eimer 1870)

Mus musculus; Levine and Becker 1933, 86.

- E. franklinii* Hall and Knipling 1936
Citellus franklinii; Iowa; Hall and Knipling 1935, 129.
- E. geomydis* Skidmore 1928
Geomys bursarius; Nebraska; Skidmore 1929, 183.
- E. irresidua* Kessel and Jankiewicz 1931
Oryctolagus cuniculus domesticus; Baltimore; Kessel and Jankiewicz 1931, 309
- E. magna* Pearard 1925
Lepus californicus c.; California; Levine and Becker 1933, 88, 97.
Oryctolagus cuniculus domesticus; Iowa; Becker 1933, 232, 234.
Sylvilagus floridanus mearnsi; Iowa; Becker 1933, 232, 234.
- E. media* Kessel and Jankiewicz 1931
Lepus californicus c.; Levine and Becker 1933, 88, 97.
Oryctolagus cuniculus domesticus; Levine and Becker 1933, 88, 97.
- E. miyairii* Becker and Hall 1931
Rattus norvegicus; Iowa; Becker and Hall 1931, 115.
- E. monacis* Fish 1930
Marmota monax monax; District of Columbia; Fish 1930, 99.
- E. neotomae* Henry 1932
Neotoma fuscipes f.; California; Henry 1932, 284.
- E. nieschulzi* Dieben 1924
Rattus norvegicus; Levine and Becker 1933, 89.
R. rattus rattus; Ibid.
- E. ondatrae-zibethicae* Martin 1930
Ondatra zibethica z.; Nebraska; Martin 1930, 273.
- E. os* Crouch and Becker 1931
Marmota monax m.; Iowa; Crouch and Becker 1931, 128.
- E. perforans* (Leuckart 1879).
Lepus americanus a.; Canada; Boughton 1932, 535.
L. californicus c.; Levine and Becker 1933, 88, 97.
Oryctolagus cuniculus domesticus; Levine and Becker 1933, 88, 97.
- E. perforoides* Crouch and Becker 1931
Marmota monax m.; Iowa; Crouch and Becker 1931, 128.
- E. princeps* (Labbe 1894)
Oryctolagus cuniculus domesticus; Levine and Becker, 1933, 88, 97.
- E. residua* Henry 1932
Neotoma fuscipes f.; California; Henry 1932, 285.
- E. schubergi* (Labbe 1896)
Mus musculus; Levine and Becker 1933, 97.
- E. sciurorum* Galli-Valerio 1922
Sciurus niger rufiventer; Iowa; Knipling and Becker 1935, 418.

- E. separata* Becker and Hall 1931
Rattus norvegicus; Iowa; Becker and Hall 1931, 131.
- E. sprehni* Yakimov 1934
Castor canadensis c.; Canada; Yakimov 1934, 294.
- E. stiedae* (Lindemann 1865)
Lepus americanus a.; Canada; Boughton 1932, 535.
L. californicus c.; Levine and Becker 1933, 88, 97.
Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.
Oryctolagus cuniculus domesticus; Cosmopolitan; Schwartz and Shook 1933, 12.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
S. f. mallurus; North Carolina; this paper.
- E. sp.*
Oryctolagus cuniculus domesticus; Canada; Boughton 1932, 524.
Sciurus griseus g.; Levine and Becker 1933, 92.
Sciurus sp.; Ibid.
- Endamoeba citelli* Becker 1926
Citellus tridecimlineatus texensis; Iowa; Becker 1926, 444.
- E. cuniculi* Brug 1918
Lepus californicus c.; Oklahoma; Ward 1934, 84.
Oryctolagus cuniculus domesticus; Wenyon 1926, 229.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
- E. hystolytica* (Schaudinn 1903)
Rattus norvegicus; South Carolina; Lynch 1915, 32.
- E. muris* (Grassi 1879).
Mus musculus; North Carolina; Harkema, this paper.
- Enteromonas intestinalis* Fonseca 1918
Lepus californicus c.; Oklahoma; Ward 1934, 84.
Oryctolagus cuniculus domesticus; Wenyon 1926, 307.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
S. f. mallurus; North Carolina; Harkema, this paper.
- Giardia beckeri* Hegner 1926
Citellus tridecimlineatus texensis; Iowa; Hegner 1926, 203.
- G. duodenalis* Davaine 1875
Lepus californicus c.; Oklahoma; Ward 1934, 84.
Oryctolagus cuniculus domesticus; Stiles and Boeck 1923, 180.
Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
- G. lamblia* Stiles 1916
Rattus norvegicus; California; Kofoid, McNeil and Bonestell 1933, 187.

- G. microti* Kofoid and Christenson 1915
Microtus californicus c.; California; Kofoid and Christenson 1915, 31.
Peromyscus leucopus leucopus; North Carolina; Harkema, this paper.
Peromyscus maniculatus gambeli; California; Kofoid and Christenson 1915, 31.
- G. muris* Grassi 1879
Mus musculus; California; Kofoid and Christenson 1915, 31.
Peromyscus maniculatus gambeli; California; Ibid.
P. m. maniculatus; California; Stiles and Boeck 1923, 180.
Rattus norvegicus; Missouri; Tsuchiya and Rector 1935, 426.
- Haemogregarina citellicola* (Wellman and Wherry 1910)
Otospermophilus grammurus beecheyi; United States; Brumpt 1913, 101.
- Hepatozoon muris* (Balfour 1905)
Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55.
R. rattus rattus; United States; Brumpt 1913, 100.
- Hexamitus marmotae* Crouch 1934
Marmota monax m.; Iowa; Crouch 1934, 513.
- H. muris* (Grassi 1881)
Rattus norvegicus; California; Kofoid, McNeil and Bonestell 1933, 187.
- H. pulcher* Becker 1926
Citellus tridecimlineatus texensis; Iowa; Becker 1926, 295.
- Sarcocystis leporum* Crawley 1914
Sylvilagus floridanus mallurus; Maryland; Crawley 1914, 214.
- S. muris* Negri 1910
Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55;
Missouri; Tsuchiya and Rector 1935, 426.
- Tetratrichomastix citelli* Becker 1926
Citellus tridecimlineatus texensis; Iowa; Becker 1926, 294.
- Trichomonas cryptonucleata* Crouch 1933
Marmota monax m.; Iowa; Crouch 1933, 297.
- T. digranula* Crouch 1933
Marmota monax m.; Iowa; Kentucky; Crouch 1933, 296.
- T. intestinalis* (Leuckart 1879)
Rattus norvegicus; South Carolina; Lynch 1915, 22, 32.
- T. marmotae* Crouch 1933
Marmota monax m.; Iowa; Kentucky; Crouch 1933, 296.
- T. muris* (Grassi 1879)
Citellus tridecimlineatus texensis; Iowa; Becker 1926, 294.
Mus musculus; United States; Stiles and Boeck 1923, 180.
Peromyscus maniculatus gambeli; California; Kofoid and Christenson 1915, 31.

- P. leucopus leucopus*; Wenrich 1921, 120.
Rattus norvegicus; California; Kofoed, McNeil and Bonestell 1933, 187;
Missouri; Tsuchiya and Rector 1935, 427.
- T. wenrichi* Crouch 1933
Marmota monax m.; Kentucky; Crouch 1933, 296.
- T. sp.*
Citellus tridecimlineatus texensis; Iowa; Becker 1926, 296.
- Trypanosoma brucei* Plimmer and Bradford 1899 (experimental)
Peromyscus californicus c.; Michigan; Packanian 1934, 139.
P. eremicus anthonyi; Ibid.
P. e. eremicus; Ibid.
P. maniculatus artemisiae; Ibid.
P. m. bairdii; Ibid.
P. m. gambeli; Ibid.
P. m. osgoodi; Ibid.
P. m. ribidus; Ibid.
P. m. sonorensis; Ibid.
P. polionotus p.; Ibid.
P. truei gilberti; Ibid.
- T. citelli* Watson 1912
Citellus richardsonii; Canada; Watson and Hadwen 1912, 24.
- T. cruzi* Chagas 1909 (experimental)
Neotoma fuscipes annectens; California; Kofoed and Donat 1933, 258.
N. f. macrotus; California; Wood 1934, 497.
P. californicus c.; California; Kofoed and Donat 1933, 258.
P. eremicus fraterculus; California; Kofoed and Donat 1933, 258.
P. maniculatus gambeli; California; Wood 1934, 497.
P. truei giloerti; California; Wood 1934, 497.
Rattus norvegicus; California; Kofoed and Donat 1933, 258.
- T. evotomys* Hadwen 1912
Evotomys gapperi saturatus; Canada; Watson and Hadwen 1912, 25.
- T. hippicum* Darling 1910 (experimental)
Coendou laenatum; Panama; Clark and Dunn 1933, 275.
Dasyprocta punctata dariensis; Ibid.
- T. hixsoni* Becker and Roudabush 1934
Citellus franklini; Iowa; Becker and Roudabush 1934, 529.
- T. iowensis* Becker and Roudabush 1934
Citellus tridecimlineatus t.; Iowa; Becker and Roudabush 1934, 527.
- T. leporis-sylvaticus* Watson 1912
Sylvilagus floridanus mallurus; Canada; Watson and Hadwen 1912, 22.
- T. lewisi* (Kent 1882)
Neotoma fuscipes macrotus; California; Wood 1934, 497.

- Rattus norvegicus*; Cosmopolitan; Watson and Hadwen 1912, 24.
Rattus rattus r.; Wenyon 1926, 463.
T. microti Laveran and Pettit 1909
Microtus californicus c.; California; Wood 1934, 499.
M. pennsylvanicus; Nebraska; Coatney 1935, 456.
T. otospermophili Wellman and Wherry 1910
Otospermophilus grammurus beecheyi; California; Wellman and Wherry, 1910, 419.
T. peromysci Watson 1912
Peromyscus maniculatus m.; Canada; Watson and Hadwen 1912, 22.
P. m. nebracensis; Ibid.
T. sp.
Lepus californicus c.; Oklahoma; Ward 1934, 84.
Sylvilagus aquaticus a.; Ibid.
Sciurus sp.; Canada; Watson and Hadwen 1912, 24.

TREMATODA

- Agomodistomum norvegicum* Loewen 1934
Rattus norvegicus; Kansas; Loewen 1934, 250.
Alariae mustelae Bosma 1931
Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.
Peromyscus leucopus noveboracensis; Michigan; Bosma 1934, 117.
Amphimerus speciosus (Stiles and Hassall 1898)
Rattus norvegicus; District of Columbia; Cram 1928, 72.
Apophallus donicum (Skrjabin and Lindtrop 1919)
Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55.
Ascotyle diminuta Stunkard and Haviland 1924
Rattus norvegicus; New York; Stunkard and Haviland 1924, 4.
Catatropis filamentis Barker 1915
Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30; Nebraska; Harrah 1922, 55.
Cladorchis subtriquetrus Rudolphi 1814
Castor canadensis c.; Canada; Swales; 1933, 474, 476.
Echinochasmus schwartzi Price 1931
Ondatra zibethica z.; Maryland; Price 1931, 4.
Echinoparyphium contigerum Barker and Bastron 1915
Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.
Echinostomum armigerum Barker and Irvine 1915
Ondatra zibethica z.; Canada; Ibid.
E. callawayensis Barker and Noll 1915
Ondatra zibethica z.; Canada; Ibid.

E. coalitum Barker and Beaver 1915

Ondatra zibethica z.; Canada; Ibid; Maryland; Krull 1935, 76.

E. revolutum (Froelich)

Ondatra zibethica z.; Canada; Swales 1933, 474.

E. sp.

Ondatra zibethica z.; Canada; Swales 1933, 480.

Entosiphonus thompsoni Sinitzin 1931

Peromyscus leucopus leucopus; North Carolina; Harkema, this paper.

P. l. noveboracensis; Maryland; Krull 1933, 49.

Fasciola hepatica Linnaeus

Castor canadensis c.; Stiles 1895, 280.

Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.

Peromyscus leucopus noveboracensis; Maryland, Krull 1933, 98.

Sylvilagus floridanus alacer; Louisiana; Dikmans 1930, 162.

S. f. mallurus; Maryland; Krull 1933, 50.

Hasstilesia texensis Chandler 1929

Lepus californicus texianus; Texas; Chandler 1929, 3.

Sylvilagus floridanus alacer; Texas; Chandler 1929, 3.

H. tricolor (Stiles and Hassall 1891)

Lepus americanus a.; Stiles and Hassall 1891, 160, 161.

Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.

Sylvilagus floridanus mallurus; Stiles and Hassall 1894, 160, 161.

Sylvilagus sp.; Alabama; Noble and Smith 1932, 216.

Hemistomum craterum Barker and Noll 1915

Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Heterochinostomum magnovatum Stunkard and Haviland 1924

Rattus norvegicus; New York; Stunkard and Haviland 1924, 7.

Monostomum sp.

Microtus pennsylvanicus p.; Stiles and Hassall 1894, 253.

Notocotyle hassalli McIntosh and McIntosh 1934

Microtus pennsylvanicus p.; Maryland; McIntosh and McIntosh 1934, 36.

N. quinqueseriale Barker and Laughlin 1915

Microtus pennsylvanicus p.; Maryland; Harrah 1922, 54.

Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30; Washington;

Harrah 1922, 54.

N. urbanensis (Cort 1914)

Ondatra zibethica z.; Maryland; Harrah 1922, 51.

Nudacotyle novicia Barker 1916

Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Paragonimus sp.

Ondatra zibethica z.; Michigan; Ameel 1932, 382.

- Paramonostomum echinum* Harrah 1922.
 Ondatra zibethica z.; Colorado; Harrah 1922, 56.
P. pseudolaeatum Price 1931
 Ondatra zibethica z.; Price 1931, 10.
Plagiorchis proximus Barker 1915
 Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.
Postharmostomum larvaei McIntosh 1934
 Tamias striatus lysteri; Michigan; McIntosh 1934, 3.
Psilostomum ondatrae Price 1931
 Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.
Renifer ellipticum Pratt 1903
 Castor canadensis c.; Philadelphia; Canavan 1934, 117.
Scaphiostomum pancreaticum McIntosh 1934
 Peromyscus gossypinus g.; Georgia; McIntosh 1935, 80.
 Tamias striatus lysteri; Michigan; McIntosh, 3.
Schistosomatum douthitti Price 1931
 Microtus pennsylvanicus p.; Price 1931, 691.
 Mus musculus; Price 1931, 691.
 Peromyscus maniculatus; Price 1931, 690.
S. pathlopticum Tanabe 1923
 Rattus norvegicus; Massachusetts; Tanabe 1923, 197.
Stephanoproraoides lawi Price 1934
 Castor canadensis c.; Canada; Price 1934, 1.
Urotrema schillingeri Price 1931
 Ondatra zibethica z.; Maryland; Price 1931, 8.
Wardius zibethicus Barker and East 1915
 Ondatra zibethica z.; Law and Kennedy 1932, 30.

CESTODA

- Andrya cuniculi* (Blanchard 1891)
 Oryctolagus cuniculus domesticus; United States; Meggitt 1924, 206.
A. macrocephala Douthitt 1915
 Geomys bursarius; Minnesota; Douthitt 1915, 10.
A. primordialis Douthitt 1915
 Evotomys gapperi galei; United States; Baer 1927, 211.
 E. g. gapperi; United States; Baer 1927, 211.
 Microtus pennsylvanicus, p.; United States; Meggitt 1924, 19.
 Sciurus hudsonicus h.; Minnesota; Douthitt 1915, 5.
Anomataenia telescopica Barker 1915
 Ondatra zibethica z.; United States; Meggitt 1924, 56.

Caenotaenia pusilla (Goeze 1782)*Rattus norvegicus*; United States; Oldham 1931, 65.*R. rattus rattus*; United States; Oldham 1931, 65.*Cittotaenia ctenoides* (Railliet 1890)*Lepus californicus c.*; Oklahoma; Ward 1934, 34.*L. sp.*; West Virginia; Weimer, Hedden and Cowdery 1934, 55.*Sylvilagus aquaticus a.*; Oklahoma; Ward 1934, 84.*S. floridanus alacer*; Oklahoma; Ward 1932, 84.*S. f. mallurus*; Pennsylvania; Smith 1908, 264.*C. pectinata* (Goeze 1782)*Erithizon dorsatum d.*; United States; Baer 1927, 211.*Lepus americanus a.*; Canada; Boughton 1932.*L. californicus c.*; United States; Meggitt 1924, 26.*L. c. melanotis*; Nebraska; Douthitt 1915, 47.*Oryctolagus cuniculus domesticus*; Baer 1927, 213.*Sylvilagus floridanus mallurus*; North Carolina; Harkema, this paper.*S. nuttalli nuttalli*; United States; Meggitt 1924, 26.*S. n. pinetis*; United States; Baer 1927, 213.*S. palustris p.*; United States; Meggitt 1924, 29.*C. praecequis* Stiles 1895*Geomys bursarius*; United States; Baer 1927, 212.*C. sp.**Geomys bursarius*; Minnesota; Douthitt 1915, 62.*Cladotaenia* sp.*Cynomys bursarius*; Scott 1931, 49.*Davainea* sp.*Geomys breviceps b.*; Oklahoma; Douthitt 1915, 62.*Diandrya composita* Darrah 1930*Marmota flaviventris nosophora*; Wyoming; Darrah 1930, 252.*Echinococcus granulosus* (Batsch 1786)*Oryctolagus cuniculus domesticus*; Hall 1919.*Hymenolepis diminuta* (Rudolphi 1819)*Mus musculus*; North Carolina; Harkema, this paper.*Rattus norvegicus*; District of Columbia; Stiles and Hassall 1894; California; McCoy 1909, 1370.*R. rattus rattus*; United States; Oldham 1930, 62.*Sigmodon hispidus h.*; United States; Meggitt 1924, 70.*S. h. texianus*; Smith 1908, 264.*H. evaginata* Barker and Andrews 1915*Ondatra zibethica z.*; Canada; Law and Kennedy 1932, 30.

- H. fraterna* (Stiles 1906)
Mus musculus; Maryland; Shorb 1933, 91.
Rattus norvegicus; Maryland; Shorb 1933, 91.
- H. nana* (Siebold 1852)
Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55;
Missouri; Tsuchiya and Rector 1935, 427.
- H. sp.*
Geomys breviceps b.; Oklahoma; Douthitt 1915, 62.
G. bursarius; Illinois; Minnesota; Dakota; Douthitt 1915, 62.
G. personatus fallax; Texas; Douthitt 1915, 62.
Ondatra zibethica z.; Canada; Swales 1933, 480.
- "Larval Tapeworm"
Cynomys leucurus; Wyoming; Scott 1930, 115.
Sciurus carolinensis c.; Maryland; Virginia; Schwartz 1928, 67.
- Mesocestoides lineatus* (Goeze 1782)
Mus musculus; Hall 1919, 61.
Rattus norvegicus; United States; Oldham 1931, 64.
- Multiceps multiceps* (Leske 1780) (larva)
Lepus americanus a.; Canada; Boughton 1932, 213.
Lepus sp.; United States; Meggitt 1924, 154.
Oryctolagus cuniculus domesticus; United States; Meggitt 1924, 154.
- M. packi* Christenson 1929 (larva)
Lepus americanus a.; Minnesota; Christenson 1929, 49.
L. californicus c.; Oklahoma; Ward 1934, 84.
L. californicus c.; Oklahoma; Ward 1934, 84.
L. campestris c.; United States; Schulz 1931, 205.
Sylvilagus floridanus mearnsi; United States; Schulz 1931, 206.
- M. serialis* (Gervais 1847) (larva)
Lepus americanus a.; Canada; Boughton 1932, 213.
L. californicus c.; United States; Hall 1919, 81.
L. c. deserticola; Ibid.
L. c. texianus; Ibid.
L. c. wallawalla; Ibid.
L. callotis; Mexico; Meggitt 1924, 155.
L. campestris c.; Meggitt 1924, 155.
Oryctolagus cuniculus domesticus; Hall 1919, 81.
Rattus norvegicus; United States; Oldham 1931, 65.
Sciurus carolinensis c.; United States; Hall 1919, 81.
S. niger neglectus; Ibid.
S. n. niger; United States; Meggitt 1924, 155.
S. n. rufiventer; Nebraska; Martin 1930, 804.

- Sylvilagus floridanus mearnsi*; United States; Bonnal, Joyeux and Bosch 1933, 1068.
S. palustris palustris; United States; Bonnal, Joyeux and Bosch 1933, 1068.
- Oochoristica* sp.
Geomys bursarius; Minnesota; Douthitt 1915, 62.
- Paroniella retractilis* (Stiles 1895)
Sylvilagus auduboni arizonae; Stiles 1895, 343.
- Paranoplocephala infrequens* (Douthitt 1915)
Exotomys sp.; North Dakota; Baer 1927, 212.
Geomys bursarius; Canada; Baer 1927, 212.
Microtus sp.; United States; Baer 1927, 212.
- Prochoanotaenia spermophili* MacLeod 1933
Citellus richardsonii; Canada; MacLeod 1933, 124.
C. tridecimlineatus t.; Canada; MacLeod 1933, 124.
- Rallietina (Johnstonia) salmonis* (Stiles 1895)
Lepus californicus melanotis; United States; Meggitt 1924, 49.
Sylvilagus floridanus mallurus; United States; Schulz 1931, 184, 185.
- R.* sp.
Geomys breviceps b.; Oklahoma; Meggitt 1924, 51.
Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 551.
- Schizotaenia americana* (Stiles 1895)
Erethizon dorsatum d.; United States; Baer 1927, 212.
E. epixanthum e., Ibid.
- S. anoplocephaloides* Douthitt 1915
Geomys breviceps b.; Oklahoma; Douthitt 1915, 35.
- S. erethizontis* (Beddard 1914)
Erethizon dorsatum d.; New York; Douthitt 1915, 33.
E. epixanthum e.; Alaska; Baer 1927, 116.
- S. sigmodontis* Chandler and Suttles 1922
Sigmodon hispidus h.; United State; Baer 1927, 211.
Sigmodon h. texianus; Texas; Chandler and Suttles 1922, 123.
- Taenia hydatigena* (Pallas 1766) (larva)
Mus musculus; District of Columbia; Stiles and Hassall 1894, 353.
Rattus norvegicus; United States; Oldham 1931, 66.
R. rattus rattus; United States; Ibid.
Sciurus niger neglectus; Hall 1919, 81.
S. n. niger; Meggitt 1924, 160.
- T. pisiformis* (Bloch 1780) (larva)
Lepus americanus a.; Canada; Boughton 1932, 213.
L. californicus c.; Oklahoma; Ward 1934, 84.
L. c. wallacvalla; California; Hall 1919, 81.

- L. sp.*; West Virginia; Weimer, Hedden and Cowdery 1934, 55.
Mus musculus; Hall 1919, 81.
Oryctolagus cuniculus domesticus; Hall 1919, 81.
Rattus rattus r.; United States; Oldham 1931, 66.
Sylvilagus auduboni baileyi; Meggitt 1924, 164.
S. floridanus alacer; Oklahoma; Ward 1934, 84.
S. f. mallurus; Hall 1919, 82.
S. f. mearnsi; Hall 1919, 82.
S. nuttalli, n.; Meggitt 1924, 164.
S. n. pinetis; Hall 1919, 82.
S. palustris palustris; Hall 1919, 82.
T. portolae (Wellman and Wherry 1910) (larva)
Otospermophilus grammurus g.; California; Meggitt 1924, 164.
Taenia taeniaeformis (Batsch 1786) (larva)
Mus musculus; California; McCoy 1909, 1370; United States; Hall 1919, 81.
Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.
Rattus norvegicus; United States; Hall 1919, 81.
Sciurus carolinensis c.; North Carolina; Harkema, this paper.
S. n. rufiventer; Kansas; Dobrovsky and Harbough 1934, 67; Nebraska; Martin 1930, 804.
T. twitchelli Schwartz 1924 (larva)
Erethizon epixanthum e.; Alaska; Schwartz 1924, 2.
T. sp.
Erethizon dorsatum d.; District of Columbia; Stiles and Hassall 1894, 334.
Sylvilagus floridanus mallurus; Ibid.
S. palustris p.; Ibid.
Weinlandia citelli MacLeod 1933
Citellus franklinii; Canada; MacLeod 1933, 122.
C. richardsonii; Ibid.
C. tridecimlineatus t.; Ibid.

NEMATODA

- Ascaris laevis* Leidy 1856
Marmota monax m.; United States; Hall 1916, 41.
Capillaria gastrica (Baylis 1926)
Rattus norvegicus; District of Columbia; Alicata and Lucker 1932, 311.
C. hepatica (Bancroft 1893)
Castor canadensis c.; District of Columbia; Chitwood 1934, 10.
Geomys bursarius; Philadelphia; Weidman 1917, 37.
Ondatra zibethica z.; Canada; Swales 1933, 475.
Rattus norvegicus; Hall 1916, 32.

- R. rattus alexandrinus*; Hall 1916, 32.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
Thomomys fessor; Wyoming; Dikmans 1932, 84.
C. ransomia Barker and Noyes 1915
Ondatra zibethica z.; Nebraska; Hall 1916, 34.
C. sp.
Cynomys leucurus ludozicianus; Ratcliffe 1931, 37.
Castorstrongylus castoris; Chapin 1925
Castor canadensis c.; District of Columbia; Chapin 1925, 681; Philadelphia; Canavan 1931, 199.
Citellina marmotae Manter 1930
Marmota monax canadensis; Maine; Manter 1930, 29.
M. m. monax; New York; McClure 1934, 49, 51, 55.
Citellinema bifurcatum Hall 1916
Citellus elegans; Colorado; Hall 1916, 142.
C. mcnaci Manter 1930
Marmota monax canadensis; Maine; Manter 1930, 29.
C. quadrivittati (Hall 1916)
Eutamias quadrivittatus q.; Colorado; Schulz 1933, 77.
C. sleggsi Manter 1930
Citellus richardsonii; Canada; Schulz 1933, 77.
Dermatoxys veligera (Rudolphi 1819)
Lepus alleni a.; Arizona; Vorhies and Taylor, 1933, 551.
L. californicus melanotis; United States; Hall 1916, 102.
Sylvilagus auduboni baileyi; United States; Hall 1916, 102.
S. nuttalli pinetis; Ibid.
Dipetalonema diacantha (Molin 1858)
Erethizon dorsatum d.; Minnesota; Jellison 1933, 43, 45.
Dirofilaria repens Railliet and Henry 1911
Erethizon dorsatum d.; Philadelphia; Canavan 1931, 223.
D. scapiceps (Leidy 1886)
Lepus campestris c.; United States; Schulz 1931, 136-137.
Sylvilagus floridanus alacer; United States; Ibid.
S. floridanus mallurus; United States; Hall 1916, 166.
S. palustris palustris; United States; Schulz 1931, 136-137.
D. spinosa Canavan 1929
Erethizon dorsatum d.; Minnesota; Jellison 1933, 43, 45.
D. subcutanea (Linstow 1899)
Erethizon dorsatum d.; Philadelphia; Canavan 1931, 221; Canada; Boulenger 1920, 492.
Filaria sp.
Castor canadensis c.; Michigan; Hall 1916, 188.

- Filaria obtusa* (Froelich 1791) *Proto spirura muris* (Gmelin 1791)
Rattus norvegicus; District of Columbia; Stiles and Hassall 1894, 339.
Gongylonema neoplasticum (Fibiger and Ditlevsen 1914)
Rattus norvegicus; District of Columbia; Lucker 1931, 55.
Gongylonema sp.
Castor canadensis c.; Michigan; Hall 1916, 198.
Graphidium strigosus (Dujardin 1845)
Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.
Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
Heligmosomum vexillatum Hall 1916
Rattus norvegicus; Colorado; Hall 1916, 157.
Thomomys fessor; Colorado; Hall 1916, 157.
Heterakis spumosa Schneider 1866
Mus musculus m.; Maryland; Winfield 1933, 177.
Rattus norvegicus; United States; Hall 1916, 47.
R. rattus rattus; Ibid.
Heteroxynema cucullatum Hall 1916
Eutamias minimus oparius; Colorado; Hall 1916, 60.
Litosomoides carinii Vaz 1934
Sigmodon hispidus h.; Mexico, Texas; Vaz 1934, 146.
L. patersoni Sandground 1934
Sigmodon sp.; Sandground 1934, 596.
L. sigmodontis Chandler 1931
Sigmodon hispidus h.; Texas; Chandler 1931, 6.
Longistriata adunca Chandler 1932
Sigmodon hispidus h.; Texas; Chandler 1932, 25, 27.
L. carolinensis Dikmans 1935
Peromyscus maniculatus nebracensis; Indiana; Dikmans 1935, 72-81.
L. dalrympei Dikmans 1935
Ondatra zibethica z.; New Jersey, Indiana, Mississippi; Dikmans 1935, 72-81.
Microtus pennsylvanicus p.; Ibid.
L. hassalli (Price 1928)
Sciurus carolinensis c.; Maryland; Price 1928, 4.
L. musculi Dikmans 1935
Mus musculus; Louisiana; Dikmans 1935, 72-81.
L. norvegicus Dikmans 1935
Rattus sp.; Louisiana; Dikmans 1935, 72-81.
L. noviberiae Dikmans 1935
Sylvilagus aquaticus littoralis; Louisiana; Dikmans 1935, 78.
S. floridanus alacer; Louisiana; Ibid.

Microfilaria sp.

Oryctolagus cuniculus domesticus; Canada; Harkin 1927, 113.

M. rosenau McCoy 1911

Otospermophilus grammurus beecheyi; California; Hall 1916, 189.

Micropleura sigmodoni Ochoterna and Caballero

Sigmodon hispidus h.; Mexico; Ochoterna and Caballero 1932, 123-125.

Monodontus floridanus McIntosh 1935

Sigmodon hispidus h.; Florida; McIntosh 1935, 29.

Nematode sp.

Lepus californicus c.; Oklahoma; Ward 1934, 84.

Nematodirus leporis Chandler 1924

Oryctolagus cuniculus domesticus; Texas; Chandler 1924, 2.

N. neotoma Hall 1916

Neotoma cinerea rupicola; Colorado; Hall 1916, 138.

N. desertorum; Colorado; Ibid.

N. floridanus baileyi; United States; Travassos 1921, 30, 70, 115.

N. mexicana fallax; United States; Hall 1916, 138.

N. sp.; Hall 1916, 138.

N. triangularis Boughton 1932

Lepus americanus a.; Canda; Boughton 1932, 532.

N. sp.

L. alleni alleni; Arizona; Vorhies and Taylor 1933, 551.

Nematospira turgida Walton 1923

Microtus pennsylvanicus p.; Illinois; Walton 1923, 61.

Nippostrongylus muris (Yokogawa 1920)

Rattus norvegicus; Maryland; Yokogawa 1920, 29.

R. rattus alexandrinus; Maryland; Graham 1934, 352.

Obeliscoides cuniculi (Grayvill 1923)

Lepus californicus c.; Oklahoma; Ward 1934, 84.

L. c. melanotis; New York; McClure 1932, 7, 14.

L. sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.

Oryctolagus cuniculus domesticus; Graybill 1923, 340.

Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.

S. floridanus alacer; Ibid.

S. f. mallurus; Graybill 1924, 1.

Ollulanus tricuspis Leuckart 1865 (larva)

Mus musculus; Hall 1916, 177.

Oxyuris tetraptera (Nitzsch 1821)

Mus musculus; United States; Hall 1916, 89.

O. triradiata Hall 1916

Ammospermophilus leucurus l.; United States; Hall 1916, 89

Callospermophilus lateralis cinerascens; United States; Hall 1916, 89.

- O. sp.*
 Microtus pennsylvanicus p.; United States; Stiles and Hassall 1894, 342.
 Pitymys pinetorum p.; Maryland; Stiles and Hassall 1894, 342.
- Passalurus ambigua* (Rudolphi 1829)
 Lepus arcticus; Hall 1916, 70.
 L. californicus c.; Oklahoma; Ward 1934, 84.
 L. sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.
 Marmota monax m.; New York; Baker 1934, 48.
 Oryctolagus cuniculus domesticus; United States; Hall 1916, 70.
 Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
 S. f. mallurus; Hall 1916, 70.
- P. nonannulatus* Skinker 1931
 Lepus americanus a.; Canada; Skinker 1931, 5.
 Sylvilagus floridanus mallurus; United States; Skinker 1931, 5.
- Physaloptera spinicauda* MacLeod 1933
 Citellus franklinii; Canada; MacLeod 1933, 122.
 C. tridecimlineatus t.; Canada; MacLeod 1933, 122.
- Protospirura ascaroidea* Hall 1916
 Geomys breviceps b.; Oklahoma; Hall 1916, 120.
 Sigmodon hispidus texianus; Oklahoma; Chandler and Suttles 1922, 123.
- P. columbiana* Cram 1926
 Rattus norvegicus; District of Columbia; Cram 1926, 3.
- P. muris* (Gmelin 1790)
 Microtus pennsylvanicus p.; Illinois; Walton 1924, 204.
 Mus musculus m.; Hall 1916, 206; Illinois; Kudo 1924, 160.
 Rattus norvegicus; United States; Hall 1916, 206.
 R. rattus alexandrinus; United States; Hall 1916, 206.
 R. r. rattus; United States; Hall 1916, 206.
- Protostrongylus rufescens*
 Sylvilagus nuttalli grangeri; Scott & Honess 1932, 60.
- Ransomus rodentorum* Hall 1916
 Thomomys fessor; Colorado; Hall 1916, 118.
- Rictularia citelli* MacLeod 1933
 Citellus franklinii; Canada; MacLeod 1933, 122.
 C. tridecimlineatus t.; Ibid.
- R. coloradensis* Hall 1916
 Eutamias quadrivittatus c.; Colorado; Hall 1916, 175.
 Peromyscus leucopus l.; North Carolina; Harkema, this paper.
- Sincosta aberrans* Roe 1929
 "Wild Mouse"; New Jersey; Roe 1929, 3.
- Spirura infundibuliformis* MacLeod 1933
 Citellus richardsonii; Canada; MacLeod 1933, 117.
 C. tridecimlineatus t.; Canada; Ibid.

Strongyloides papillosus (Wedl 1856)

Lepus americanus a.; Canada; Boughton 1932, 530.

Oryctolagus cuniculus domesticus; United States; Ransom 1911, 105.

Rattus norvegicus; United States; Hall 1916, 8; Canada; Boughton 1932, 530.

S. ratti Sandground 1925

Rattus norvegicus; Maryland; Sandground 1925, 71; Missouri; Tsuchiya and Rector 1935, 427.

Strongylus sp.

Castor canadensis c.; United States; Hall 1916, 109.

Synthetocaulus commutatus (Diesing 1851)

Oryctolagus cuniculus domesticus; Schwartz and Shook 1933, 22.

S. leporis Boughton 1932

Lepus americanus a.; Canada; Boughton 1932, 533-534.

S. rufescens (Leuckart 1865)

Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.

Syphacia obvelata (Rudolphi 1802)

Evotomys gapperi g.; United States; Hall 1916, 82.

Mus musculus m.; Ibid.

Neotoma mexicana fallax; Ibid.

Onychomys leucogaster l.; Ibid.

Peromyscus nasutus; Ibid.

Rattus norvegicus; Ibid.

R. rattus rattus; Ibid.

Syphacia peromysci n. sp.

Peromyscus leucopus leucopus; North Carolina; Harkema, this paper.

S. thompsoni Price 1928

Glaucomys volans v.; Virginia; Price 1928, 2.

Travassosius americana Chapin 1925

Castor canadensis c.; District of Columbia; Chapin 1925, 679.

Trichinella spiralis (Owen 1835)

Oryctolagus cuniculus domesticus; United States; Stiles and Hassall 1894, 349.

Rattus norvegicus; United States; Hall 1916, 10.

R. rattus rattus; United States; Hall 1916, 10.

Trichosomoides crassicauda (Bellingham 1845)

Rattus norvegicus; United States; Oldham 1931, 78.

R. rattus rattus; United States; Oldham 1931, 78.

Trichostrongylus affinis Graybill 1924

Sylvilagus floridanus mallurus; Graybill 1924, 1.

T. calcaratus Ransom 1911

Oryctolagus cuniculus domesticus; Graybill 1924, 1.

- Sylvilagus floridanus alacer*; Oklahoma; Ward 1934, 84.
S. f. mallurus; Maryland; Ransom 1911, 367.
T. colubriiformis (Giles 1892)
Lepus californicus melanotis; Nebraska; Skidmore 1932, 800.
Sciurus aberti aberti; United States; Hall 1916.
Sciurus a. minus; United States; Nagaty 1932, 470.
T. fiberius Barker and Noyes 1915
Ondatra zibethica z.; Nebraska; Hall 1916, 129.
T. retortaeformis (Zeder 1800)
Oryctolagus cuniculus domesticus; United States; Travassos 1921, 15, 41, 115.
T. sp.
Marmota monax m.; New York; McClure 1934, 49.
Trichuris fossor Hall 1916
Thomomys fossor; Colorado; Hall 1916, 23.
T. leporis (Froelich 1789)
Oryctolagus cuniculus domesticus; United States; Hall 1916, 25.
Lepus americanus a.; Canada; Boughton 1932, 539.
Lepus sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.
Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.
S. floridanus f.; United States; Hall 1916, 25.
S. f. mallurus; United States; Hall 1916, 25.
T. opaca Barker and Noyes 1915
Ondatra zibethica z.; Nebraska; Hall 1916, 28.
Vestibulozetaria patersoni (Mazza 1923)
Sigmodon hispidus h.; Mexico; Vogel and Gabaldon 1932, 124.
Warrenius bifurcatus Hall 1916
Citellus richardsonii; Canada; MacLeod 1933, 144.
W. quadrivittati Hall 1916
Eutamias quadrivittatus c.; Colorado; Hall 1916, 144.
Wellcomia evoluta (Linstow 1899)
Erethizon dorsatum d.; Philadelphia; Canavan 1931, 208.
E. epixanthum c.; Minnesota; Jellison 1933, 44.
Sylvilagus floridanus mearnsi; Kansas; Danheim 1924, 124.

ACANTHOCEPHALA

Acanthocephalid

- Lepus americanus*; Manitoba; Boughton 1932, 527, 539.
Moniliformis moniliformis (Bremser 1811)
Rattus norvegicus; Chandler 1921, 179.
R. rattus r.; Ibid.
Sciurus niger n.; Stiles and Hassall 1894e, 352.

M. spiradentatus MacLeod 1933

Citellus tridecemlineatus t.; Canada; MacLeod 1933, 121.

M. sp.

Neotoma sp.; Florida; Stiles 1932, 90.

Sciurus niger n.; Texas; Chandler 1921, 179.

PENTASTOMIDA

Linguatula serrata (Froelich 1789)

Oryctolagus cuniculus domesticus; Schwartz and Schook 1933.

Porocephalus sp.

Erethizon dorsatum d.; Stiles and Hassall 1894, 354.

PARASITIC MITES

Atricholaelaps glasgowi (Ewing 1925)

Sciurus carolinensis c.; North Carolina; Harkema, this paper.

Bdella cardinalis Banks

Rattus norvegicus; New York; Fox and Sullivan 1925, 17.

Cyclolaelaps circularis Ewing 1932

Peromyscus truei t.; Utah; Ewing 1933, 6.

Cytolaelaps banksi Wellman and Wherry 1910

Otospermophilus grammurus beecheyi; California; Wherry and Wellman 1910, 421.

C. penrosei Weidman 1916

Cynomys ludovicianus l.; Philadelphia; Weidman 1916, 82.

Dermanyssus evotomydis Ewing 1933

Evotomys sp.; New York; Ewing 1933, 11, 13.

Echinolaelaps echidninus Berlese

Mus musculus; Cosmopolitan; Banks 1910, 84.

Rattus norvegicus; Ibid.

R. rattus *rattus*; Ibid.

Euhaemogamasus americanus (Banks 1906)

Peromyscus eremicus e.; Arizona; Banks 1906, 137.

E. microti Ewing 1925

Microtus pennsylvanicus p.; New York; Ewing 1925, 142.

E. onychomydis Ewing 1933

Onychomys sp.; Arizona; Ewing 1933, 4.

E. oregonensis Ewing 1933

Dicrostonyx hudsonicus; Oregon; Ewing 1933, 5.

Phenacomys albipes; Oregon; Ibid.

E. sanguineus (Ewing and Stover 1915)

Rattus rattus rattus; Iowa; Ewing and Stover 1915, 111.

E. twitchelli (Ewing 1925)

Evotomys dawsoni d.; Alaska; Ewing 1925, 143.

- E. utahensis* Ewing 1933
Neotoma lepida L.; Utah; Ewing 1933, 41.
- E. alaskensis* (Ewing 1925)
Microtus sp.; Alaska; Ewing 1925, 138.
- Hannemania hirsuta* Ewing 1931
Perognathus californicus c.; California; Ewing 1931, 18.
- Ichoronyssus carnifex* (Koch)
Mus sp.; Oregon; Ewing 1923, 15.
- I. isabellensis* (Oudemans)
Mus sp.; District of Columbia; Ewing 1923, 16.
- I. sternalis* Ewing 1923
Marmota monax m.; Plimmers Island; Ewing 1923, 14.
- Laelaps hawaiiensis* Ewing
Rattus rattus r.; New York, New Orleans; Fox and Sullivan 1925, 1909.
- L. hollisteri* Ewing 1925
Peromyscus californicus c.; California; Ewing 1925, 2.
- L. multispinosus* Banks
Ondatra zibethica z.; Banks 1915, 84.
- L. protheticus* Banks
Marmota monax m.; Banks 1915, 84.
- Liponyssus bacoti* (Hirst)
Rattus norvegicus; District of Columbia, New York, Missouri, Texas;
Ewing 1922, 19.
- L. montanus* Ewing 1922
Citellus richardsoni; Montana, Canada; MacLeod 1933, 112.
C. tridecimlineatus t.; Ibid.
- L. occidentalis* Ewing 1922
Citellus richardsoni; Montana, Canada; MacLeod 1933, 112.
C. tridecimlineatus t.; Ibid.
- Listrophorus validus* Banks
Ondatra zibethica z.; Banks 1915, 127.
- Myobia musculi* Shrank
Mus musculus m.; United States; Banks 1910, 84.
- M. ratti* Skidmore 1932
Rattus norvegicus; Nebraska; Skidmore 1932, 172.
- Neoschongastia brevipes* Ewing 1931
Peromyscus leucopus noveboracensis; Maryland; Ewing 1931, 16.
- N. californicus* (Ewing 1925)
"Ground Squirrel"; California; Ewing 1931, 5.
- N. peromysci* (Ewing 1929)
Peromyscus leucopus noveboracensis; Massachusetts; Ewing 1931, 5.
- N. sciuricola* (Ewing 1925)
Sciurus hudsonicus richardsoni; Montana; Ewing 1931, 5.

Notoedres notodres (Megnin)*Rattus norvegicus*; United States; Ewing 1929, 54.*R. rattus rattus*; United States; Ibid.*N. sp.**Sciurus griseus g.*; California; Bryand 1921, 128.*Psoroptes communis cuniculi* (Delafond)*Oryctolagus cuniculus domesticus*; Schwartz and Shook 1933, 3.*Lepus californicus c.*; Oklahoma; Ward 1934, 83.*Sylvilagus aquaticus a.*; Oklahoma; Ward 1934, 83.*S. floridanus alacer*; Oklahoma; Ibid.*Sarcoptes scabiei* De Geer*Rattus norvegicus*; California; McCoy 1909, 1371.*Schizocarpus mingaudi* Trouessart 1896*Castor canadensis c.*; Banks 1915, 127.*Tetragonyssus microti* Ewing 1933*Microtus californicus c.*; California; Ewing 1933, 10.*M. sp.*; California; Ibid.*T. spiniger* (Ewing and Stover 1915)*Ondatra rivalicia*; Louisiana; Svihla 1930, 287.*O. zibethica z.*; United States; Ewing 1923, 11.*Trombicula bisignalia* Ewing 1929*Microtus pennsylvanicus p.*; Maine; Ewing 1929, 295.*Peromyscus maniculatus abietorum*; Maine; Ibid.*T. dentata* Ewing 1925*Sigmodon hispidus chiriquensis*; Panama; Ewing 1925, 260.*T. dunni* Ewing 1931*Dasyprocta punctata nuchalis*; Panama; Ewing 1931, 112.*T. harperi* Ewing 1928*Evotomys gapperi g.*; New York; Ewing 1928, 79.*Napaeozapus insignis i.*; New York; Ibid.*Sciurus hudsonicus h.*; New York; Ibid.*T. irritans* (Riley)*Lepus californicus c.*; Oklahoma; Ward 1934, 83.*Sylvilagus aquaticus a.*; Oklahoma; Ibid.*S. floridanus alacer*; Oklahoma; Ibid.*T. microti* Ewing 1928*Microtus pennsylvanicus modestus*; Colorado; Ewing 1928, 80.*M. richardsoni macropus*; Wyoming; Ibid.*T. panamensis* Ewing 1925*Sigmodon hispidus chiriquensis*; Panama; Ewing 1925, 260.*Trombicula sp.**Sciurus carolinensis c.*; North Carolina; Harkema, this paper.

IXODOIDEA

- Amblyomma longirostre* Koch
 Coendou rothschildi; Panama; Dunn 1923, 98.
- A. maculatum* Koch 1844
 Lepus californicus merriami; Texas; Bishopp 1912, 37.
- A. parvus* Aragao 1908
 Sigmodon hispidus chiriquensis; Panama; Dunn 1923, 99.
- Dermacentor albipictus* Packard
 Oryctolagus cuniculus domesticus; Bishopp and Wood 1913, 163.
- D. andersoni* Stiles (D. VENUSTUS Banks)
 Callospermophilus chrysodeirus c.; United States; Brumpt 1922, 758.
 C. lateralis cinerascens; Western United States; Hooker, Bishopp and Wood 1912, 166.
 Citellus columbianus c.; Montana; Cooley 1932, 47, 50.
 C. franklini; MacLeod 1933, 111.
 C. richardsonii; Canada, Montana; Ibid.
 C. tridecimlineatus t.; Canada; Ibid.
 Erethizon epixanthum c.; Jellison 1933, 43.
 Eutamias amoenus lutriventris; Montana; Cooley 1932, 32.
 E. umbrinus; Montana; Ibid.
 Lepus bairdii b.; Western United States; Hooker, Bishopp and Wood 1912, 166.
 L. campestris townsendi; United States; Brumpt 1922, 758.
 Marmota flaviventris f.; Western United States; Hooker, Bishopp and Wood 1912, 166.
 M. monax m.; Western United States; Ibid.
 Microtus pennsylvanicus modestus; Western United States; Ibid.
 M. nanus canescens; Western United States; Ibid.
 Neotoma cinerea c.; Western United States; Ibid.
 Ochotona princeps p.; Western United States; Ibid.
 Sciurus hudsonicus richardsoni; Western United States; Ibid.
 Sylvilagus nuttalli n.; Western United States; Ibid.
 Thomomys fuscus f.; Western United States; Ibid.
- D. electus* Linnaeus
 Lepus callotis; Neumann 1901b, 365.
 L. sp.; Ibid.
- D. occidentalis* Neumann 1899
 Otospermophilus grammurus beecheyi; Wherry and Wellman 1909, 376.
- D. perumapertus marginatus* Banks
 Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 550.
 L. californicus; Arizona; Ibid.
 L. c. deserticola; Utah; Stanford 1934, 247.
 L. c. melanotis; Colorado; McCampbell 1926, 12.

D. variabilis (Say)

Microtus pennsylvanicus p.; Massachusetts; Parker, Philip and Jellison 1933, 349.

Peromyscus leucopus; Montana; Cooley 1932, 15; Massachusetts; Parker, Philip and Jellison 1933, 349.

Sciurus niger n.; Western United States; Hooker, Bishopp and Wood 1912, 191.

Sylvilagus aquaticus a.; Western United States; Ibid.

Haemaphysalis concinna Koch 1844

Marmota monax m.; Neumann 1901, 365.

H. flava Neumann 1897

Lepus sp.; Neumann 1901, 365.

H. leporis-palustris (Packard 1869)

Lepus americanus a.; Canada; Hewitt 1915, 230.

L. californicus c.; Oklahoma; Ward 1934, 83.

L. c. melanotis; Colorado; McCampbell 1926, 12.

L. sp.; United States; Neumann 1901, 365.

Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933, 27.

Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 83.

S. floridanus alacer; Oklahoma; Ibid.

S. f. mallurus; North Carolina; this paper.

S. palustris p.; United States; Neumann 1901, 364.

Ixodes aequalis Banks 1909

Otospermophilus grammurus beecheyi; California; Wherry and Wellman 1909, 376.

I. angustus Neumann 1901

Lepus americanus a.; Canada; Hewitt 1915, 226.

Neotoma cinerea occidentalis; United States; Neumann 1901, 365.

Sciurus douglasii d.; Canada; Hadwen 1911, 37.

S. d. vancouverensis; Canada; Ibid.

I. a. woodi Bishopp 1911

Neotoma micropus m.; Texas; Nuttall 1916, 336.

I. banksi Bishopp 1911

Ondatra zibethica z.; Arkansas; Nuttall 1916, 337.

I. dentatus Marx 1899

Oryctolagus cuniculus domesticus; Neumann 1901, 324.

I. d. spinipalpis Hadwen and Nuttall 1915

Lepus americanus a.; Canada; Nuttall 1916, 304.

Sciurus douglasii; Canada; Ibid.

I. diversifossus Neumann 1899

Sylvilagus nuttalli n.; Montana; Bishopp 1912, 30.

S. n. grangeri; Utah; Stanford 1934, 247.

- I. hexagonus* Leach 1815
Sylvilagus floridanus; Neumann 1901, 365.
- I. hexagonus cookei* (Packard 1869)
Callospermophilus chrysodeirus; San Francisco; Nuttall 1916, 328.
- I. hexagonus inchoatus* Neumann 1901
Sciurus sp.; Neumann 1901, 365.
- I. hexagonus* (Leach) *longispinosus* Neumann 1901
Marmota sp.; Neumann 1901, 365.
- I. holocyclous* Neumann 1899
Sciurus sp.; Neumann 1901, 365.
- I. kingi* Bishopp 1911
Citellus columbianus c.; Hooker, Bishopp, and Wood 1912, 82.
Cynomys gunnisoni g.; Colorado; Burnett and McCampbell 1926, 7.
Dipodomys ordii richardsoni; Hooker, Bishopp, and Wood 1912, 82.
Sciurus hudsonicus richardsoni; Ibid.
Thomomys talpoides clusius; Ibid.
Ochotona princeps p.; Ibid.
- I. loricatus* Neumann 1899
Neotoma cinerea occidentalis; Idaho; Neumann 1901, 172.
- I. marxi* Banks 1908
Lepus californicus; Oklahoma; Ward 1934, 32.
- I. pratti* Banks 1908
Thomomys sp.; California; Banks 1908, 28.
- I. ricinus* (Linnaeus)
Lepus cuniculus; Neumann 1901, 364.
Rattus norvegicus; Neumann 1901, 364.
Sylvilagus floridanus mallurus; Neumann 1901, 365.
- I. sculptus* Neumann 1904
Citellus tridecemlineatus t.; Iowa, Wyoming; Hixson 1932, 36, 42.
Cynomys gunnisoni g.; Colorado; Burnett and McCampbell 1926, 7.
- I. texanus* Banks 1909
Sciurus hudsonicus richardsoni; Bishopp 1912, 32.
- I. sp.*
Lepus californicus deserticola; Utah; Stanford 1934, 247.
Sciurus hudsonicus richardsoni; Montana; Birdseye 1912, 12.
- Margaropus annulatus* (Say)
Rattus norvegicus; United States; Banks 1910.
- Ornithodoros talaji* Guern
Rattus norvegicus; Dunn 1933, 477, 498.
R. rattus; Ibid.

MALLOPHAGA

- Eutrichophilus coendu* Stobbe 1913
Coendou mexicanum mexicanum; Mexico; Harrison 1916, 73.

E. setosus (Giebel)*Erethizon dorsatum d.*; Minnesota; Fenstermacher and Jellison 1932, 294.*Trichodectes geomydis* Osborn*Dipodomys merriami m.*; Arizona; Kellogg and Ferris 1915, 73.*Geomys bursarius*; Ibid.*C. cumberlandius*; Ferris 1916, 99.*Thomomys bottae b.*; Kellogg and Ferris 1915, 73.*T. bulbivorus*; California; Paine 1912, 437.*T. monticola m.*; California; Ferris 1916, 99.*T. sp.*; California; Kellogg and Ferris 1915, 73.

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Enderleinellus extremus Ferris 1919*Sciurus colliae c.*; Mexico; Ferris 1919.*S. deppei d.*; Mexico; Ibid.*S. griseoflavus chiapensis*; Mexico; Ibid.*S. negligens*; Mexico; Ibid.*S. nelsoni*; Mexico; Ibid.*S. poleopis p.*; Mexico; Ibid.*E. kelloggi* Ferris 1916*Sciurus goldmani*; Mexico; Ferris 1919, 22.*S. griseus nigripes*; California; Ibid.*S. griseus g.*; California; Ibid.*E. longiceps* Kellogg and Ferris 1915*Sciurus aberti ferreus*; Nebraska; Ferris 1919, 19.*S. apache*; Mexico; Ibid.*S. arizonensis huachua*; Ferris 1916, 148, 191.*S. carolinensis c.*; Mississippi; Ferris 1919, 19.*S. kaibabensis*; Arizona; Ibid.*S. niger n.*; Nebraska, Indiana; Ibid.*S. n. rufiventer*; Nebraska; Ibid.*S. oculatus*; Mexico; Ibid.*E. marmotae* Ferris 1919*Marmota monax rufescens*; South Dakota; Ferris 1919, 47.*E. nitzschi* Fahrenholz 1916*Sciurus douglasii albolimbatus*; California; Ferris 1919, 10.*S. d. mollipilosus*; California; Ibid.*S. fremonti f.*; Colorado; Ibid.*S. hudsonicus petulans*; Alaska; Ferris 1919, 9.*S. h. vancouverensis*; Alaska; Ferris 1919, 10.*S. sp.*; Ferris 1919, 10.*E. osborni* Kellogg and Ferris 1915*Citellus beldingi*; Texas; Ferris 1919, 46.

- Otospermophilus grammurus beecheyi*; California; Kellogg and Ferris 1915, 71.
O. g. douglasii; California; Ferris 1919, 46.
O. g. fisheri; California; Ibid.
O. g. grammurus; Arizona; Ibid.
- E. suturalis* (Osborn 1891)
Ammospermophilus leucurus l.; Colorado; Ferris 1919, 43.
A. nelsoni nelsoni; California; Ibid.
Callospermophilus chrysodeirus c.; California; Ibid.
C. lateralis castanurus; Utah; Ibid.
Citellus beldingi; California; Ibid.
C. elegans; Colorado; Ibid.
C. franklinii; Iowa, North Dakota; Ibid.
C. mollis mollis; Nevada; Ibid.
C. oregonus; Nevada; Ferris 1916, 149, 187.
C. osgoodi; Alaska; Ferris 1919, 43.
C. townsendii; Washington; Ibid.
C. tridecimlineatus pallidus; Kansas; Ibid.
C. t. texensis; Oklahoma; Ibid.
C. t. tridecimlineatus; Iowa; Ibid.
Cynomys gunnisoni g.; Colorado; Ibid.
C. leucurus; Colorado, Wyoming; Ibid.
Otospermophilus grammurus g.; Arizona; Ibid.
- Fahrenholzia microcephala* Ferris 1922
Heteromys goldmani; Mexico; Ferris 1922, 161.
Liomys irroratus canus; Mexico; Ibid.
L. i. texensis; Mexico; Ibid.
L. pictus obscurus; Mexico; Ibid.
- F. pinnata* Kellogg and Ferris 1915
Dipodomys deserti d.; California; Kellogg and Ferris 1915, 73.
D. herrmanni californicus; California; Ibid.
D. merriami m.; California; Ferris 1916, 150.
D. ordii richardsoni; Oklahoma; Ibid.
D. ornatus; Mexico; Ferris 1922, 160.
D. philippsii; Mexico; Ibid.
D. sp.; Ferris 1916, 150, 193.
Perognathus parvus olivaceus; Nevada; Ferris 1922, 160.
- F. tribulosa* Ferris 1916
Perognathus californicus c.; California; Ferris 1916, 102, 1922, 163.
P. formosus; California; Ibid.
- F. t. reducta* Ferris 1922
Perognathus formosus; California; Ferris 1922, 166.

F. t. zacatecae Ferris 1922

Perognathus hispidus zacatecae; Mexico; Ferris 1922, 166.

Haematopinoides squamosus Osborn 1891

Geomys bursarius; Iowa; Ferris 1916, 180, 194.

Haemodipsus leporis

Lepus californicus c.; Oklahoma; Ward 1934, 83.

H. lyriocephalus (Burmeister)

Lepus arcticus a.; Ferris 1932, 330.

H. setoni Ewing 1924

Lepus californicus c.; California; Ewing 1924, 550.

L. c. melalnotis; Kansas; Ibid.

L. campestris c.; Ferris 1932, 336.

H. ventricosus (Denny)

Lepus californicus c.; California; Kellogg and Ferris 1915, 74.

L. c. deserticola; Arizona; Ibid.

L. campestris c.; Iowa; Ibid.

Oryctolagus cuniculus domesticus; Ibid.

Hoplopleura acanthopus acanthopus (Burmeister 1839)

Lagurus intermedius; Nevada; Ferris 1916, 154.

Microtus californicus c.; California; Ferris 1921, 64.

M. c. constrictus; California; Ibid.

M. nanus nanus; Utah; Stanford 1934, 247.

M. sp.; California; Iowa; Ferris 1921, 64.

Neotoma cinerea c.; California; Ibid.

Pitymys pinetorum p.; New York, Iowa; Ibid.

Synaptomys sp.; Canada; Ibid.

H. erratica arboricola (Kellogg and Ferris 1915)

Eutamias merriami pricei; California; Ferris 1921, 109.

E. speciosus frater; California; Ibid.

E. toxensendii alleni; California; Ibid.

E. t. ochrogenys; California; Ibid.

E. sp.; California; Ibid.

Tamias striatus striatus; California; Ibid.

H. e. erratica (Osborn 1896)

Eutamias alpinus; California; Ferris 1921, 108.

Tamias striatus striatus; California; Ibid.

H. hesperomydis (Osborn 1891)

Mus musculus m.; California; Ferris 1916, 112.

Onychomys leucogaster arcticeps; Colorado; Ibid.

O. torridus longicaudus; California; Ferris 1921, 72.

O. t. pulcher; California; Ferris 1916, 112.

Oryzomys fulvestrus; Mexico; Ferris 1921, 72.

- Peromyscus boylei* b.; California; Ferris 1921, 71.
P. leucopus l.; Iowa; Ibid.
P. maniculatus gambeli; Utah, California; Ibid.
P. m. maniculatus; Iowa; Ibid.
P. m. rubidus; California; Ibid.
- H. hirsuta* Ferris 1916
Sigmodon hispidus eremicus; Arizona, California; Ferris 1916, 112; 1921, 117.
S. h. hispidus; North Carolina; Ibid.
S. h. texianus; Texas; Ibid.
S. ocregnathus; Mexico; Ibid.
Xenomys nelsoni nelsoni; Mexico; Ibid.
- H. nesoryzomydis* Ferris 1921
Zygodontomys seorsus; Panama; Ferris 1921, 90.
- H. quadridentata* (Neumann 1904)
Oryzomys fulvescens f.; Mexico; Ferris 1921, 88.
O. rostratus r.; Mexico; Ibid.
- H. sciuricola* Ferris 1921
Sciurus arizonensis huachua; Arizona; Ferris 1921, 110.
S. carolinensis c.; Florida, Mississippi; Ibid.
S. douglasii albolimbatus; California; Ibid.
S. d. douglasii; California; Ibid.
S. d. mollipilosus; California; Ibid.
S. griseus g.; California; Ibid.
S. hudsonicus h.; Alaska; Ibid.
S. h. vancouverensis; Alaska; Ibid.
S. kaibabensis; Arizona; Ibid.
S. sp.; Ibid.
- H. trispinosa* Kellogg and Ferris 1915
Glaucomys sabrinus lascivus; Oregon; Ferris 1921, 115.
G. volans volans; Maryland; Ibid.
Glaucomys sp.; California; Kellogg and Ferris 1915, 72.
- Linognathoides inornatus* Kellogg and Ferris 1915
Neotoma cinerea c.; California; Ferris 1923, 252.
- Linognathoides montanus* (Osborn)
Citellus armatus; Utah; Stanford 1934, 247.
C. beldingi; California; Ferris 1916, 99.
C. columbianus c.; Washington; Ferris 1916, 159.
C. mexicanus m.; Mexico; Ibid.
C. mollis m.; Utah; Stanford 1934, 247.
C. oregonus; Nevada; Ferris 1916, 99.
C. parryi kennicotti; Alaska; Ferris 1916, 159.

- C. plesius ablusus*; Alaska; Ferris 1916, 100.
C. sp.; Colorado; Ferris 1916, 159.
Cynomys leucurus l.; Colorado; Ferris 1916, 99.
Marmota flaviventris engelhardti; Utah; Stanford 1934, 24.
M. f. sierrae; Colorado, California; Ferris 1916, 159.
M. sp.; Oregon; Kellogg and Ferris 1915, 72.
Otospermophilus grammurus beecheyi; California; Ibid.
O. g. douglasii; California; Ferris 1916, 159.
O. g. grammurus; Arizona; Ferris 1916, 100; Utah; Stanford 1934, 247.
Sciurus niger neglectus; Ferris 1916, 100.
- Linognathus piliferus* (Burmeister)
Lepus washingtoni w.; California; Ewing 1924, 548.
- Microphthirus uncinata* (Ferris 1916)
Glaucomys sabrinus lascivus; California; Ferris 1919, 49.
- Neohacmatopinus inornatus* (Kellogg and Ferris 1915)
Neotoma cinerea occidentalis; Ferris 1923, 252.
- N. laevisculus* (Grube)
Callospermophilus lateralis castanurus; Utah; Ferris 1923, 264-265.
Citellus beldingi; California; Ibid.
C. columbianus c.; Washington; Ibid.
C. elegans; Colorado; Ibid.
C. mexicanus m.; Mexico; Ibid.
C. oregonus; Oregon; Ibid.
C. osgoodi; Alaska; Ibid.
C. parryi kennicottii; Alaska; Ibid.
C. plesius ablusus; Alaska; Ibid.
Cynomys leucurus; Colorado; Ibid.
Marmota flaviventris f.; Oregon; Ibid.
Otospermophilus grammurus beecheyi; Ibid.
O. g. beecheyi; California; Ibid.
O. g. grammurus; Arizona; Ibid.
- N. marmotae* Ferris 1923
Marmota flaviventris f.; California; Ferris 1923, 267.
M. sp.; Montana; Ibid.
- N. pacificus*; Kellogg and Ferris 1915
Eutamias alpinus; California; Ferris 1923, 249.
E. merriami pricei; California; Ibid.
E. speciosus frater; California; Ibid.
E. toxensendii alleni; California; Ibid.
E. t. oregonensis; California; Ibid.
E. t. sonomae; Ibid.

- N. sciurinus sciurinus* (Mjöberg)
 Hodomys alleni; Mexico; Ferris 1923, 244.
 Neotoma fuscipes streator; California; Ibid.
 Sciurus aberti ferreus; Colorado; Ibid.
 S. apache; Mexico; Ibid.
 S. carolinensis c.; Mississippi; Ibid; North Carolina; Harkema, this paper.
 S. coliaei c.; Mexico; Ferris 1923, 244.
 S. deppei d.; Mexico; Ibid.
 S. douglasii albolimbatus; California; Ibid.
 S. douglasii d.; California; Ibid.
 S. d. mollipilosus; California; Ibid.
 S. griseus g.; California; Ibid.
 S. g. nigripes; California; Ibid.
 S. hudsonicus richardsoni; Montana; Ibid.
 S. nelsoni n.; Mexico; Ibid.
 S. niger neglectus; California; Ibid.
 S. n. rufiventer; Iowa, Indiana, Nebraska; Ibid.
 S. oculatus c.; Mexico; Ibid.
 S. poliopus p.; Mexico; Ibid.
N. sciurinus griseicolus Ferris 1923
 Sciurus griseus g.; California; Ferris 1923, 248.
N. sciuropteri Ferris 1916
 Glaucomys sabrinus lascivus; California; Ferris 1916, 170.
 G. volans v.; Iowa; Ibid.
 G. sp.; California, Ferris 1923, 241.
N. sp.
 Glaucomys volans v.; North America; Enderlein 1904, 143.
Philandesia foxi Ewing
 Marmota flaviventris; Washington; Ewing 1927, 87.
 Rattus norvegicus; New York City; Ewing 1927, 87.
Polyplax alaskensis Ewing 1927
 Microtus sp.; Alaska; Ewing 1927, 119.
P. auricularis Kellog and Ferris 1915
 Peromyscus maniculatus gambeli; Ferris 1916, 172.
 P. m. rubidus; Ferris 1916, 155.
 P. sitkensis prevostensis; Alaska; Ferris 1916a, 99, 172.
 P. truei t.; Utah; Stanford 1934, 247.
P. auricularis Kellog and Ferris 1915
 Neotomodon alstoni; Mexico; Ferris 1923, 219.
 Onychomys leucogaster articeps; Colorado; Ferris 1916, 172, 197.
 O. torridus pulcher; Colorado; Ibid.
 Reithrodentomys mexicanus m.; Mexico; Ferris 1923, 219.

P. spinulosa (Burmeister)

- Lagurus intermedius*; Nevada; Ferris 1916a, 99.
Microtus californicus c.; California; Ferris 1916, 176.
M. sp.; California; Ferris 1923, 187, 188.
Phenacomys longicaudus; California; Ferris 1916, 176.
Rattus norvegicus; Ferris 1916, 176.
R. rattus alexandrinus; United States; Ibid.
R. r. r.; Panama, United States; Ibid.
Synaptomys borealis; Canada; Ferris 1923, 128.

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Amphipsylla pollionis (Rothschild 1905)

- Evotomys gapperi saturatus*; Canada; Jordan and Rothschild 1913, 406.
Microtus drummondi d.; Canada; Ibid.

Anomipsylla nudatus Baker 1898

- Neotoma albigula a.*; Arizona; Baker 1904, 426, 452.
Rattus sp.; California; Fox 1925, 217.

Atyphloceras bishopi Jordan 1933

- Microtus pennsylvanicus p.*; New York; Jordan 1933a, 65.

A. felix Jordan and Rothschild 1915

- Mus sp.*; Arizona; Jordan and Rothschild 1915, 60.
Peromyscus truei t.; New York; Jordan 1933, 69.

Carteretta carteri Fox 1927

- Neotoma fuscipes f.*; California; Fox 1927, 210.

Catallagia charlottensis (Baker 1898)

- Eutamias amoenus luteiventris*; Montana; Dunn and Parker 1923, 2775.
Lepus bairdii b.; Montana; Ibid.
Peromyscus maniculatus artemisiae; Montana; Ibid.
P. m. macrochirus; Canada; Rothschild 1915, 43.

C. decipiens Rothschild 1915

- Evotomys gapperi saturatus*; Canada; Rothschild 1915, 43.
Neotoma cinerea c.; Canada; Ibid.

Cediopsylla inaequalis (Baker 1895)

- Citellus columbianus c.*; Montana; Dunn and Parker 1923, 2775.
Lepus bairdii b.; Montana; Ibid.
Lepus californicus melanotis; Colorado; McCampbell 1926, 12.
L. campestris c.; Montana; Dunn and Parker 1923, 2775.
L. sp.; Arizona, Colorado, Idaho; Baker 1904, 439.
Sciurus hudsonicus richardsoni; Montana; Ibid.
S. floridanus alacer; Oklahoma; Ward 1934, 83.
S. nuttalli n.; Montana; Dunn and Parker 1923, 2775.

C. i. interrupta; Jordan 1925

- Sylvilagus bachmani b.*; California; Jordan 1925, 103.

- Cediopsylla simplex* (Baker 1895)
 Lepus sp.; North Carolina; Shaftesbury 1934, 253.
 Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 83.
 S. f. floridanus; Eastern United States; Jordan 1925, 103.
 S. f. mallurus; North Carolina; Shaftesbury 1934, 253.
- Ceratophyllus adustus* Jordan 1932
 Erethizon epixanthum e.; Canada; Jordan 1932, 255.
- C. apachensis* Fox 1914
 Cynomys ludovicianus arizonensis; New Mexico; Fox 1914, 15.
- C. divinus* (Baker 1898)
 Sciurus fremonti f.; Colorado; Baker 1904, 441.
 S. hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
- C. multidentatus* Fox 1909
 Microtus californicus c.; California; Fox 1909, 107.
- C. niger inflexus* Jordan 1929
 Eutamias sp.; Colorado; Jordan 1929, 37.
- C. n. niger* Fox 1908
 Rattus norvegicus; California; Fox 1908, 434.
- C. stimsoni* Fox 1914
 Thomomys sp.; California; Fox 1914, 14.
- C. terinus* Baker
 Citellus columbianus c.; United States; Baker 1905.
- Conorhinopsylla stanfordi* Stewart 1930
 Sciurus hudsonicus h.; New York; Stewart 1930, 179.
- Ctenocephalides canis* (Bouche 1835)
 Lepus sp.; North Carolina; Ibid.
 Mus musculus; California; Fox 1908, 1371.
 Oryctolagus cuniculus domesticus; North Carolina; Shaftesbury 1934, 252.
 Rattus norvegicus; Fox 1908, 1371.
 R. rattus rattus; Ibid.
- Ctenocephalides felis* (Bouche 1835)
 Glaucornys volans v.; North Carolina; Shaftesbury 1934, 252.
 Lepus californicus c.; Arizona; Vorhies and Taylor 1933, 550.
 Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933, 10.
 Rattus norvegicus; California; Fox 1909, 1371.
 Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 83.
 S. f. mallurus; North Carolina; Shaftesbury 1934, 252.
- Ctenocephalus gigas* (Kirby)
 Lepus sp.; Michigan; Baker 1904, 421.
- Ctenophthalmus genalis* Baker 1904
 Geomys bursarius; Michigan; Baker 1904, 424.

C. pseudagyrtes Baker 1904*Evotomys gapperi* g.; Pennsylvania; Jordan 1928, 186.*Geomys bursarius*; Michigan; Baker 1904, 421.*Microtus drummondi*; Canada; Baker 1905, 154.*M. pennsylvanicus* p.; New York; Jordan 1928, 186.*M. sp.*; North Carolina; Shaftesbury 1934, 254.*Mus musculus* m.; Pennsylvania; Jordan 1928, 186.*Neotoma pennsylvanica*; Pennsylvania; Ibid.*Pitymys pinctorum* p.; Plimmers Island; Ibid.*Peromyscus leucopus* l.; Ibid.*Ctenopsyllus alpinus* (Baker 1895)*Neotoma* sp.; Colorado; Baker 1904, 452.*C. catatina* Jordan 1928*Microtus pennsylvanicus* p.; Jordan 1929a, 174.*C. mexicanus* (Baker 1896)*Rattus rattus* r.; Mexico; Baker 1904, 452.*C. ravalliensis* Dunn and Parker 1923*Neotoma cinerea* c.; Montana; Dunn and Parker 1923, 2775.*C. segnis* (Schonherr 1816)*Mus musculus* m.; United States; Fox 1908c, 1371.*Rattus norvegicus*; Ibid.*Rattus rattus rattus*; Ibid.*Sigmodon hispidus* h.; North Carolina; Shaftesbury 1934, 256.*C. selensis* (Rothschild 1908)*Evotomys gapperi* g.; Canada; Rothschild 1906, 324.*Microtus drummondi*; Canada; Ibid.*Peromyscus maniculatus* m.; Tennessee; Shaftesbury 1934, 257.*Dactylopsylla comis* Jordan 1929*Thomomys fuscus* f.; Canada; Jordan 1929, 38.*Diamanus montanus* (Baker 1895)*Citellus* sp.; Baker 1906, 162.*Otospermophilus grammurus beecheyi*; California; Fox 1908, 1565.*Rattus norvegicus*; California; Fox 1908, 1565.*Sciurus aberti* a.; Colorado; Baker 1904, 445.*S. sp.*; Jordan and Rothschild 1914, 259.*Dolichopsylla stylosus* (Baker 1903)*Aplodontia rufa* r.; Oregon, Baker 1904, 447.*Doratomyssa blarinae* Fox 1914*Mus musculus* m.; Pennsylvania; Jordan 1928, 186.*Peromyscus leucopus* l.; Ibid.*Echidnophaga gallinacea* (Westwood 1875)*Mus musculus* m.; California; Fox 1909, 1371.

- Rattus norvegicus*; North Carolina; Shaftesbury 1934, 248.
R. rattus rattus; California; Fox 1909, 1371.
Foxella ignotus apachensis (Baker 1895)
Thomomys talpoides agrestis; Colorado; 1915, 56.
F. ignotus ignotus (Baker 1895)
Geomys bursarius; Iowa; Jordan 1929, 33.
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F. ignotus franciscanus (Roths 1910)
Otospermophilus grammurus beecheyi; California; Jordan and Rothschild 1915, 45-60.
Thomomys bottae b.; California; Jordan and Rothschild 1915, 45-60.
F. ignotus recula (Baker 1895)
Thomomys talpoides t.; Canada; Jordan and Rothschild 1913, 56.
Hoplopsyllus affinis Baker 1905.
Lepus alleni a.; Arizona; Vorhies and Taylor, 550.
L. bairdii b.; Montana; Dunn and Parker 1923, 2775.
L. californicus melanotis; Colorado; MacCampbell 1926, 12.
L. sp.; Baker 1904, 32.
Sylvilagus nuttalli n.; Dunn and Parker 1923, 2775.
H. anomalus Baker 1903
Lepus californicus californicus; Oklahoma; Ward 1934, 83.
Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933, 12.
Otospermophilus grammurus beecheyi; United States; Brumpt 1922, 828.
Rattus norvegicus; California; Fox 1908, 1565.
Sylvilagus aquaticus; Oklahoma; Ward 1934, 83.
H. foxi Ewing 1924
Sylvilagus bachmani; California; Ewing 1924, 350.
H. glacialis (Tasch 1880)
Lepus arcticus a.; Greenland; Jordan 1932, 117.
H. glacialis lynx (Baker 1904)
Lepus americanus macfarlani; Canada; Jordan 1932, 253.
Hystriophylla americana Baker 1899
Evotomys gapperi g.; Maine; 1904, 454.
E. sp.; Maine; Baker 1904, 432, 454.
H. sp.
Microtus californicus c.; California; Fox 1909, 11.
H. dippiei Rothschild
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Peromyscus maniculatus austerus; Ibid.
Sciurus hudsonicus richardsoni; Montana; Ibid.
H. gigas (Baker 1904)
Sylvilagus floridanus f.; Canada, Michigan; Baker 1904, 450.

- H. gigas tahuvuana* Jordan 1929
Microtus pennsylvanicus p.; Jordan 1929, 174.
Peromyscus leucopus noveboracensis; New York; Jordan 1933, 65.
- H. mammoth* Chapin 1921
Aplodontia rufa californica; California; Chapin 1921, 26.
- Leptopsylla adelpha* Rothschild 1915
Mus sp.; Arizona; Rothschild 1915, 305.
- L. hesperomys* (Baker 1904)
Peromyscus leucopus l.; Pennsylvania; Jordan 1928, 186.
P. leucopus noveboracensis; New York; Jordan 1933a, 65.
P. sp.; New Hampshire; Baker 1904, 452.
- Malareus bitterrootensis* (Dunn and Parker 1923)
Mus sp.; Canada; Jordan 1925, 110.
Neotoma cinerea cinerea; Montana; Dunn and Parker 1923, 2775.
- M. eremicus* (Baker 1904)
Peromyscus eremicus e.; Arizona; Jordan 1933, 442.
- M. penicilliger* (Grube 1852)
Peromyscus maniculatus borealis; Jordan 1932, 253.
- M. sinomus* (Jordan 1925)
Mus. sp.; Arizona; Jordan 1925, 180.
- M. telchinum* (Rothschild 1905)
Eutamias gapperi g.; Baker 1906, 161.
Microtus californicus c.; California; Fox 1909, 10.
M. mordax m.; Dunn and Parker 1923, 2775.
Peromyscus maniculatus artemisiae; Montana; Dunn and Parker 1923, 2775.
Sylvilagus nuttalli n.; Montana; Dunn and Parker 1923, 2775.
- Megabothris abantis* (Rothschild 1905)
Microtus drummondi; Canada; Baker 1905, 146.
- M. asio* (Baker 1904)
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- M. groenlandicus* (Wahlgren 1903)
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- M. lucifer* (Rothschild 1905)
Microtus drummondi; Canada; Baker 1905, 149.
- M. megacolpus* (Jordan 1925)
Microtus drummondi; Canada; Jordan 1929, 33.
M. quirini (Rothschild 1905)
Eutamias gapperi g.; Canada; Baker 1905, 15.
E. g. saturatus; Canada; Baker 1905, 15.
Microtus drummondi, Jordan 1932, 253.
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- Megarhroglossus bisetis* Jordan and Rothschild 1915
Neotoma sp.; New Mexico; Jordan and Rothschild 1915, 54.
- M. longispinosus* Jordan and Rothschild 1915.
Mus sp.; Canada; Jordan and Rothschild 1915, 54.
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- Micropsylla peromyscus* Dunn and Parker 1923
Peromyscus maniculatus artemisiae; Montana; Dunn and Parker 1923, 2775.
- Monopsyllus anisus* (Rothschild 1907)
Rattus norvegicus; California; Rothschild 1910a, 94.
- M. ciliatus* (Baker 1904)
Eutamias luteiventris; Montana; Dunn and Parker 1923, 2775.
E. sp.; California; Baker 1904, 441.
Sciurus hudsonicus richardsoni; Dunn and Parker 1923, 2775.
- M. ciliatus protinus* (Jordan 1929)
Eutamias townsendii t.; Canada; Jordan 1929, 34.
Sciurus hudsonicus h.; Canada; Jordan 1929, 34.
- M. eumolpi eumolpi* (Rothschild 1905)
Citellus columbiana; Montana; Dunn and Parker 1923, 2775.
Eutamias affinis; Baker 1906, 162.
E. luteiventris l.; Montana; Dunn and Parker, 2775.
Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
Microtus drummondi; California; Jordan 1932, 253.
- M. vison* (Baker 1904)
Citellus columbianus c.; Montana; Dunn and Parker 1923, 2775.
Sciurus hudsonicus h.; Maine; Baker 1904, 408.
S. h. richardsoni; Montana; Dunn and Parker 1923, 2775.
- M. wagneri* (Baker 1904)
Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.
Mus musculus; Idaho; Baker 1904, 405.
Peromyscus leucopus l.; Idaho; Baker 1904, 448.
P. maniculatus artemisiae; Montana; Dunn and Parker 1923, 2775.
Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
Sylvilagus nuttalli n.; Montana; Dunn and Parker 1923, 2775.
- M. w. systaltus* (Jordan 1929)
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- Neopsylla faceta* Rothschild 1915
Sciurus hudsonicus h.; Massachusetts; Rothschild 1915, 34.
- N. hamiltoni* Dunn and Parker 1923
Neotoma cinerea c.; Montana; Dunn and Parker 1923, 2775.
- N. inopina* Rothschild 1915
Citellus columbianus c.; Montana; Dunn and Parker 1923, 2775.

- Evotomys gapperi saturatus*; Canada; Rothschild 1915, 32, 44.
Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.
Marmota flaviventris f.; Montana; Dunn and Parker 1923, 2775.
- N. similis*
Peromyscus maniculatus rufinus; New Mexico; Chapin 1919, 59.
- N. texanus* Stewart 1930
Rattus norvegicus; Texas; Stewart 1930, 180.
- N. wenmanni* (Rothschild 1904)
Neotoma cinerea c.; Canada; Baker 1905, 154.
Peromyscus leucopus; Massachusetts; Jordan 1928, 186.
P. leucopus l.; Tennessee; Shaftesbury 1934, 257.
P. l. noveboracensis; New York; Jordan 1933, 65.
Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
- Nosopsyllus fasciatus* (Bosc 1801)
Mus musculus; California; Fox 1909, 1371.
Microtus californicus c.; California; Baker 1904, 440.
Neotoma pennsylvanica p.; Jordan 1928, 183.
Peromyscus leucopus l.; Boston; Jordan 1928, 183.
Rattus norvegicus; North Carolina; Shaftesbury 1934, 255. California; Fox 1908, 1371.
Rattus rattus alexandrinus; Cosmopolitan; Banks 1910, 75.
R. rattus rattus; Ibid.
Thomomys bottae b.; Fox 1909, 10.
- Nosopsyllus londiniensis* (Rothschild 1903)
Rattus norvegicus; California; Baker 1906, 161.
R. rattus rattus; California; Banks 1910, 75.
- Odontopsyllus charlottensis* (Baker 1898)
Evotomys gapperi saturatus; Canada; Baker 1905, 145.
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Neotoma cinerea c.; Canada; Baker 1905, 162.
Lepus bairdii b.; Arizona; Dunn and Parker 1925, 2775.
Peromyscus maniculatus arcticus; Canada; Baker 1905, 162.
P. leucopus l.; Canada; Ibid.
- O. multispinosus* (Baker 1898)
Lepus californicus c.; Oklahoma; Ward 1934, 32.
Sylvilagus floridanus mallurus; North Carolina; Shaftesbury 1934, 254.
- O. spenceri*; Dunn and Parker 1923
Lepus bairdii; Montana; Dunn and Parker 1923, 2775.
Sylvilagus nuttalli n.; Dunn and Parker 1923, 2775.
- O. telegoni*; Rothschild
Evotomys gapperi g.; Baker 1905, 146.
Microtus drummondi; Canada; Tiraboschi 1907, 617.

- O. wymani* Fox 1909
Microtus californicus c.; California; Fox 1909, 241.
- Opisocrostitis bruneri* (Baker 1895)
Citellus columbianus c.; Colorado, Idaho, Nebraska; Baker 1904, 440.
C. franklini; Idaho; Nebraska; MacLeod 1933, 112.
C. richardsoni; Canada; MacLeod 1933, 112.
C. tridecimlineatus t.; Canada; MacLeod 1933, 112.
Citellus sp.; Montana; MacLeod 1933, 112.
- O. hirsutus* (Baker 1895)
Cynomys ludovicianus l.; Colorado; Baker 1904, 443.
- O. saundersi* Jordan 1933
Citellus richardsonii; Canada; Whitehead 1933, 751.
- O. tuberculatus* (Baker 1904)
Citellus columbianus c.; Idaho; Baker 1904, 393; Montana; Dunn and Parker 1923, 2775.
Marmota flaviventris f.; Montana; Dunn and Parker 1923, 2775.
Sciurus hudsonicus richardsonii; Montana; Ibid.
- Opisodasys keeni* (Baker 1896)
Peromyscus maniculatus keeni; Queen Charlotte Islands; Baker 1904, 444.
- O. pseudarctomys* (Baker 1904)
Glaucomys sabrinus alpinus; Montana; Dunn and Parker 1923, 2775.
Marmota monax m.; New York; Baker 1904, 446.
- O. pseudarctomys acasti* (Baker 1905)
Glaucomys sabrinus s.; Canada; Baer 1905, 150.
- O. robustus* (Jordan 1925)
Sciurus aberti a.; Jordan 1925, 105.
- O. vesperalis* (Jordan 1929)
Glaucomys sabrinus alpinus; Canada; Jordan 1929, 26.
- Orchopeas caedens durus* (Jordan 1925)
Sciurus hudsonicus h.; Canada; Jordan 1929, 29.
S. h. richardsoni; Canada; Jordan 1929, 29.
- O. leucopus* (Baker 1904)
Peromyscus leucopus l.; New York; Baker 1904, 445.
P. l. noveboracensis; Jordan 1933, 62.
- O. sexdentatus agilis* (Roths 1905)
Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.
Neotoma cinerea c.; Canada; Jordan 1929, 30.
Ochotona princeps; Montana; Dunn and Parker 1923, 2775.
Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
S. h. baileyi; Canada; Baker 1906, 162.
Sylvilagus nuttalli n.; Dunn and Parker 1923, 2775.

- O. s. pennsylvanicus* (Jordan 1928)
Neotoma pennsylvanica p.; Pennsylvania, Maryland, Virginia; Jordan 1928, 184.
- O. s. schiscentus* (Jordan 1929)
Neotoma sp.; Arizona; Jordan 1929, 31.
- O. wickhami* (Baker 1895)
Erethizon epixanthum e.; Minnesota; Jellison 1933, 43.
Eutamias luteiventris; Montana; Dunn and Parker 1923, 2775.
Eutamias gapperi saturatus; Baker 1905, 150.
Glaucomys volans v.; North Carolina; Shaftesbury 1934, 252.
Marmota monax m.; Pennsylvania; Jordan 1928, 183.
Sciurus carolinensis c.; Arizona, Georgia, Iowa, Nebraska, Michigan, New York; Baker 1904, 448.
S. fremonti f.; Baker 1904, 448.
S. hudsonicus h.; United States; Baker 1904, 448.
Sciurus h. richardsoni; Montana; Dunn and Parker, 2775.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 83.
Peromyscus maniculatus arcticus; Baker 1906, 162.
- Oropsylla alaskensis* (Baker 1904)
Citellus parryi kennicotti; Alaska; Baker 1904, 394, 440.
- O. arctomys* (Baker 1904)
Marmota monax; New York; Baker 1904, 440.
M. m. rufescens; New York; Jordan 1933a, 62.
- O. idahoensis* (Baker 1904)
Callospermophilus lateralis cinerascens; Montana; Dunn and Parker 1923, 2775.
Citellus columbianus c.; Idaho; Baker 1904, 413.
C. nebulicola; Alaska; Fox 1927, 212.
Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.
Marmota flaviventris; Montana; Dunn and Parker 1923, 2775.
Neotoma cinerea c.; Montana; Dunn and Parker 1923, 2775.
Sciurus aberti a.; Arizona, Alberta; Baker 1905, 150.
Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
Sylvilagus nuttalli n.; Montana; Dunn and Parker 1923, 2775.
- O. rupestris* (Jordan 1929)
Citellus richardsoni; Canada; Jordan 1929, 32.
Thomomys sp.; Canada; Jordan 1929, 32.
- Phalacroscylla arachis* Jordan 1929
Dipodomys merriami m.; Arizona; Jordan 1929, 38.
- P. paradisea*; Jordan and Rothschild 1915
Mus sp.; Rothschild 1916, 33.
Rattus sp.; Arizona; Fox 1925, 217.

- P. shannoni* Jordan 1929
Peroognathus sp.; Washington; Jordan 1929, 39.
- Pulex sp.*
Lepus californicus melanotis; Colorado; MacCampbell 1926, 12.
- P. dugesii* Baker 1899
Lepus californicus c.; Oklahoma; Ward 1934, 83.
Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 32.
- P. irritans* Linnaeus 1758
Lepus sp.; North Carolina; Shaftesbury 1934, 250.
Oryctolagus cuniculus domesticus; Ibid.
Rattus norvegicus; California; Fox 1908, 1371.
R. rattus r.; California; Fox 1908, 1371.
Sciurus carolinensis c.; North Carolina; Shaftesbury 1934, 350.
Sylvilagus floridanus mallurus; North Carolina; Shaftesbury 1934, 250.
- Rhadinopsylla sectilis* Jordan and Rothschild 1923
Mus sp.; Canada; Jordan and Rothschild 1923, 315.
- Rhopalopsyllus dunni* Jordan and Rothschild 1922.
Sigmodon hispidus chiriquensis; Panama; Jordan and Rothschild 1923a, 337.
- R. qweyni* Fox 1914
Rattus norvegicus; Georgia; Fox 1914, 11.
- R. sigmodoni* Stewart 1930
Rattus norvegicus; Texas; Stewart 1930, 177.
Sigmodon hispidus h.; Texas; Stewart 1930, 177..
- Stenoponia wetmorei* Chapin 1922
Peromyscus leucopus l.; Virginia; Shaftesbury 1934, 248.
P. l. noveboracensis; Canada; Chapin 1922, 54.
- Tarsopsylla coloradensis* (Baker 1895)
Sciurus fremonti f.; Colorado; Baker 1904, 441.
- Thrassis acamantis* (Rothschild 1905)
Marmota flaviventris f.; Montana; Dunn and Parker 1923, 2775.
Marmota f. avara; Montana; Dunn and Parker 1923, 2775.
- T. arizonensis* (Baker 1898)
Neotoma albigula a.; Arizona; Baker 1904, 440.
Citellus sp.; Arizona; Baker 1904, 412, 446.
- T. arizonensis littoris* (Jordan 1929)
Citellus tridecimlineatus t.; California; Jordan 1929, 31.
- T. bacchi* (Rothschild 1905)
Citellus tridecimlineatus texianus; Baker 1906, 162.
- T. fatus* (Jordan 1925)
Citellus tridecimlineatus t.; Colorado; Stewart 1930, 152.
- T. francisi* (Fox 1924)
Citellus mollis mollis; Utah; Fox 1927, 211.

- T. gladiolis* (Jordan 1925)
Ammospermophilus leucurus cinnamomeus; Utah; Jordan 1930, 269.
Citellus tridecimlineatus t.; California; Jordan 1925, 108.
Perognathus sp.; California; Jordan 1925, 108.
- T. gladiolis caducus* (Jordan 1930)
Ammospermophilus leucurus cinnamomeus; Utah; Jordan 1930, 269.
- T. howelli*
Marmota flaviventris sierrae.
- T. pansus* (Jordan 1925)
Citellus sp.; Arizona; Jordan 1925, 109.
- Xenopsylla cheopis* (Rothschild 1903)
Mus musculus m.; North Carolina; Shaftesbury 1934, 250.
Rattus norvegicus; Cosmopolitan; Shaftesbury 1934, 250.
Rattus rattus; Cosmopolitan; Fox 1908, 1371.
Sigmodon hispidus h.; North Carolina; Shaftesbury 1934, 249.

HEMIPTERA

- Triatoma protracta* (Uhler 1894)
Neotoma fuscipes streator; Utah; Brumpt 1922, 811.

HYMENOPTERA

- Brachymeria fonscolombei* (Dufour)
Lepus californicus texianus; Texas; Roberts 1933, 158.

DIPTERA LARVAE

- Bogeria buccata*
Mus musculus; Ohio; Miller 1928, 13.
- B. ruficus* Austen 1933
Lepus sp.; Arizona, Colorado, New Mexico, Oregon; Austen 1933, 713.
- Cochliomyia macellaria* Fab.
Lepus californicus texianus; Texas; Roberts 1933, 157.
- Cuterebra aldrichi* Austen 1933
Neotoma fuscipes f.; California; Austen 1933, 705.
- C. americana* Townsend
Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 550.
L. californicus c.; Arizona; Ibid.
- C. cuniculi* Townsend
Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933.
- C. emasculator* Fitch 1859
Sciurus hudsonicus petulans; Seguy 1924, 365.
S. h. hudsonius; Bau 1906, 25.
S. carolinensis leucotis; Seguy 1924, 355.
Tamias striatus lysteri; Canada; Cameron 1926, 430.

- C. fontinella* Clark
 Peromyscus leucopus l.; North Carolina; Harkema, this paper.
 P. l. noveboracensis; Boston; Johnson 1930, 283.
 Sylvilagus floridanus mallurus; Smith 1908, 270.
 S. nuttalli n.; New Mexico; Seguy 1924, 366.
- C. grisea* Coquilliet
 Mus musculus; Canada; Cameron 1926, 431.
- C. lepusculi* Townsend 1897
 Sylvilagus nuttalli n.; New Mexico; Seguy 1924, 366.
- C. princeps*
 Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 550.
 L. californicus c.; Arizona; Ibid.
 L. callotis; Bau 1906, 27.
- C. scudderi* Townsend
 Lepus californicus texianus; Texas; Roberts 1933, 157.
- C. tenebrosa* Coquilliet
 Cynomys ludovicianus l.; Montana; Parker and Wells 1919, 101.
 Neotoma cinerea c.; Montana; Parker and Wells 1919, 100.
 Onychomys leucogaster arcticeps; Montana; Ibid.
- C. sp.*
 Lepus artemisia; New Mexico; Townsend 1892, 299.
 Neotoma fuscipes macrotis; California; Gander 1929, 57.
 Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933.
 Rattus norvegicus; Canada; Cameron 1926, 432.
 Sylvilagus floridanus alacer; Oklahoma; Leonard 1933, 270.
 S. nuttalli n.; New Mexico; Townsend 1892, 299.
 S. palustris p.; Brauer 1803, 224-228.
- Dermatobia* sp.
 Lepus callotis; New Mexico; Townsend 1892, 299.
- D. cyaniventris* Macquart 1849
 Lepus callotis; Seguy 1924, 366.
- D. hominis* (Linnaeus)
 Dasyprocta punctata dariensis; Panama; Dunn 1934, 225.
 D. p. isthmica; Panama; Ibid.
- Sarcophaga plinthopyga* Wied.
 Lepus californicus texianus; Texas; Roberts 1933, 157.
- S. sulcata* Aldrich
 Lepus californicus texianus; Texas; Roberts 1933, 158.
- Wohlfahrtia vigil* (Walker)
 Sylvilagus floridanus mallurus; Johannsen 1926, 156.

APPENDIX II

DESCRIPTION OF A NEW SPECIES OF NEMATODE FROM THE WHITE-FOOTED MOUSE

A nematode is described in this section. This parasite belongs to the family Oxyuridae Cobbold 1864, subfamily Syphaciinae Railliet 1916, and genus *SYPHACIA* Seurat 1916. For this species the name *Syphacia peromysci* is proposed. Dr. B. G. Chitwood of the Bureau of Animal Industry, United States Department of Agriculture, kindly examined the specimens and diagnosed them as a new species of *SYPHACIA*.

Syphacia peromysci nov. sp.

Members of the genus *SYPHACIA* are slender, milk white forms. The male is much smaller than the female and the tail of both sexes is long and slender. The cuticle is coarsely striated transversely. The mouth is provided with

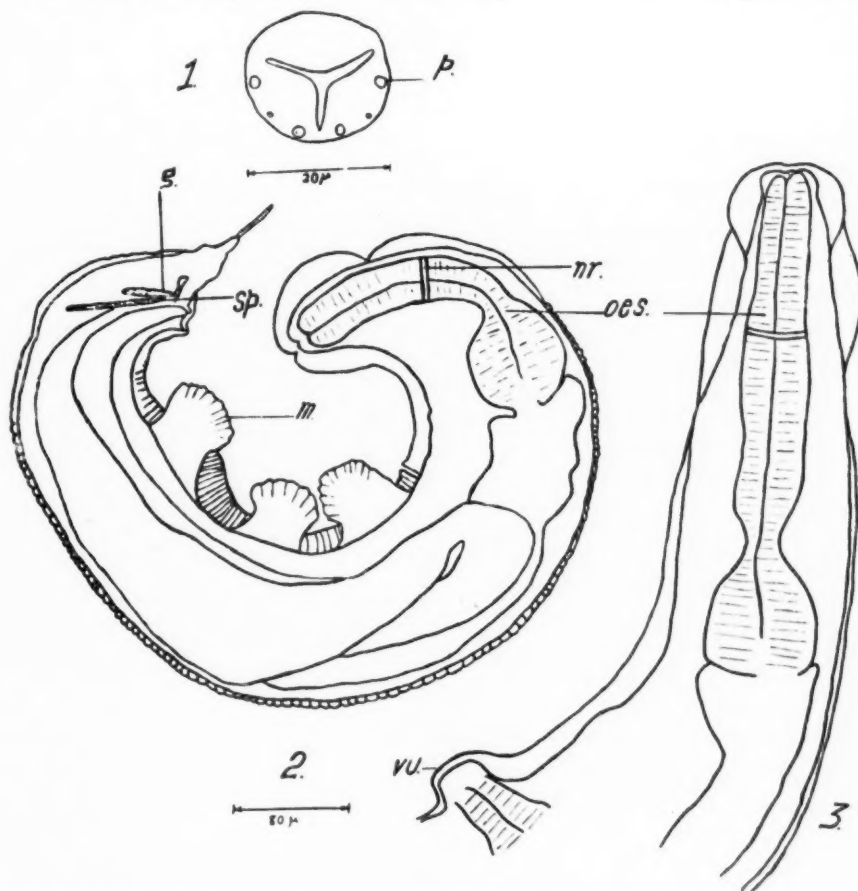


FIG. 5. *Syphacia peromysci* nov. sp.; 1. Head, end face view; 2. Adult male, entire; 3. Adult female, anterior end.

g — gubernaculum
m — mamelon

nr — nerve ring
oes — oesophagus
p — papilla

sp — spicule
vu — vulva

three lips of about equal size. The circumoral papillae are situated laterally in two groups consisting of a large papilla situated on each side of a smaller submedian one (Fig. 5, 1).

The male is 913 micra to 1.3 mm. long and 120-124 micra wide. The cuticle of the anterior end is inflated and extends to the cervical papillae. The oesophagus is typically oxyuroid, 140 to 150 micra long by 30 micra wide. The oesophageal bulb is spherical, 66 to 80 micra in diameter and is joined to the oesophagus by a slender constriction. The nerve ring surrounds the oesophagus approximately 90 micra from the anterior end of the oesophagus. The excretory pore opens ventrally approximately 172 micra from the anterior end of the body. The cervical papillae are situated approximately 60 micra from the head. Lateral alae are present beginning at the cervical papillae. There are two small symmetrical bursal alae and three pairs of caudal papillae. The spicule is simple, 70 micra long and 3 to 4 micra wide. The gubernaculum is 37 micra long by 5 micra wide and the accessory piece is 20 micra long. The ventral surface of the body bears three striated mamelons, which extend approximately 27 micra beyond the cuticle. They are approximately 50 micra long (Fig. 5, 2).

The female is 2 to 2.5 mm. long with a maximum width of 0.172 mm. The oesophagus including the bulb is 353 micra long by 46 micra wide at the widest point. The oesophageal bulb is 80 micra in diameter. The nerve ring is 97 micra from the anterior end of the oesophagus. The anus is situated 525 to 700 micra from the tip of the tail. The vulva is situated on a cuticular prominence 507 to 534 micra from the anterior end (Fig. 5, 3). The eggs are oval 80 to 81 micra long by 24 micra wide.

Host: *Peromyscus leucopus leucopus*.

Location: Caecum.

Locality: Duke Forest, Durham, North Carolina.

Syphacia peromysci resembles *Syphacia obvelata* (Rudolphi 1802), the type species of the genus, in body form and the number of mamelons in the male. It differs in that the former species is smaller than the latter in many respects. The mamelons extend beyond the cuticle to a greater distance than do those of *S. obvelata*. The eggs are much larger in the type species being 100 to 142 micra long by 30 to 40 micra wide. *Syphacia peromysci* can be separated from *S. thompsoni* Price 1928 by its smaller size. The species is readily distinguished from *S. pallargi* (Seurat 1915) and *S. pearsei* Baylis 1928 by the number of ventral mamelons, there being but two in these species.

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THE "BIG WOODS" OF MINNESOTA: ITS STRUCTURE,
AND RELATION TO CLIMATE, FIRE, AND SOILS

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THE "BIG WOODS" OF MINNESOTA: ITS STRUCTURE, AND RELATION TO CLIMATE, FIRE, AND SOILS

INTRODUCTION

Minnesota includes parts of three of the principal plant formations of North America. The southwestern and westerly portions of the state are overlapped by the grasslands. The northeastern corner belongs phytogeographically to the boreal conifer forest. Separating these two is a belt of deciduous forest, extending diagonally across the state from the southeast to the northwest (Fig. 1). The present study concerns a portion of the deciduous forest.

When the early French explorers came into the central part of Minnesota, they recognized a portion of the deciduous forest, some 3,030 square miles in extent, as being decidedly superior to the adjacent woodlands on all sides. The timber was very dense; the trees were much taller and of species different from those of the surrounding oak forest and oak savanna. In referring to this rather definite area they used the names 'Bois Grand' or 'Bois Fort' which shortly thereafter were translated as 'Big Woods' (Fig. 1).

The Big Woods is a forest community dominated by sugar maple (*Acer saccharum* Marsh.)¹ and basswood (*Tilia americana* L.). Although it was not the only stand of sugar maple-basswood forest in Minnesota, the Big Woods was the largest continuous area of such timber in the state. Numerous other tracts occur in the remainder of the deciduous forest, some in contiguous portions of the boreal conifer forest, and some about lakes and large rivers in the adjacent prairie.

Since the term "Big Woods" was apparently applied by the French to a timbered area dominated by sugar maple and basswood, it has often been applied since then to all tracts of this type of forest regardless of their location in Minnesota. The more restricted meaning is used by the writer because it defines the portion of the sugar maple-basswood community which was studied.

With the rapid settling of Minnesota in the last century, the forests have been cleared to such an extent that now the Big Woods is represented only by scattered woodlots, most of which are heavily pastured, and a very few near-virgin stands. The present study is an attempt to analyse from the phytosociological viewpoint the best remnants of the primeval forest which still exist, to reconstruct the original boundaries of the Big Woods, and to solve the distributional problems involved.

¹ The nomenclature for woody plants follows Rosendahl and Butters (1928), and for herbaceous plants, Robinson and Fernald (1908).

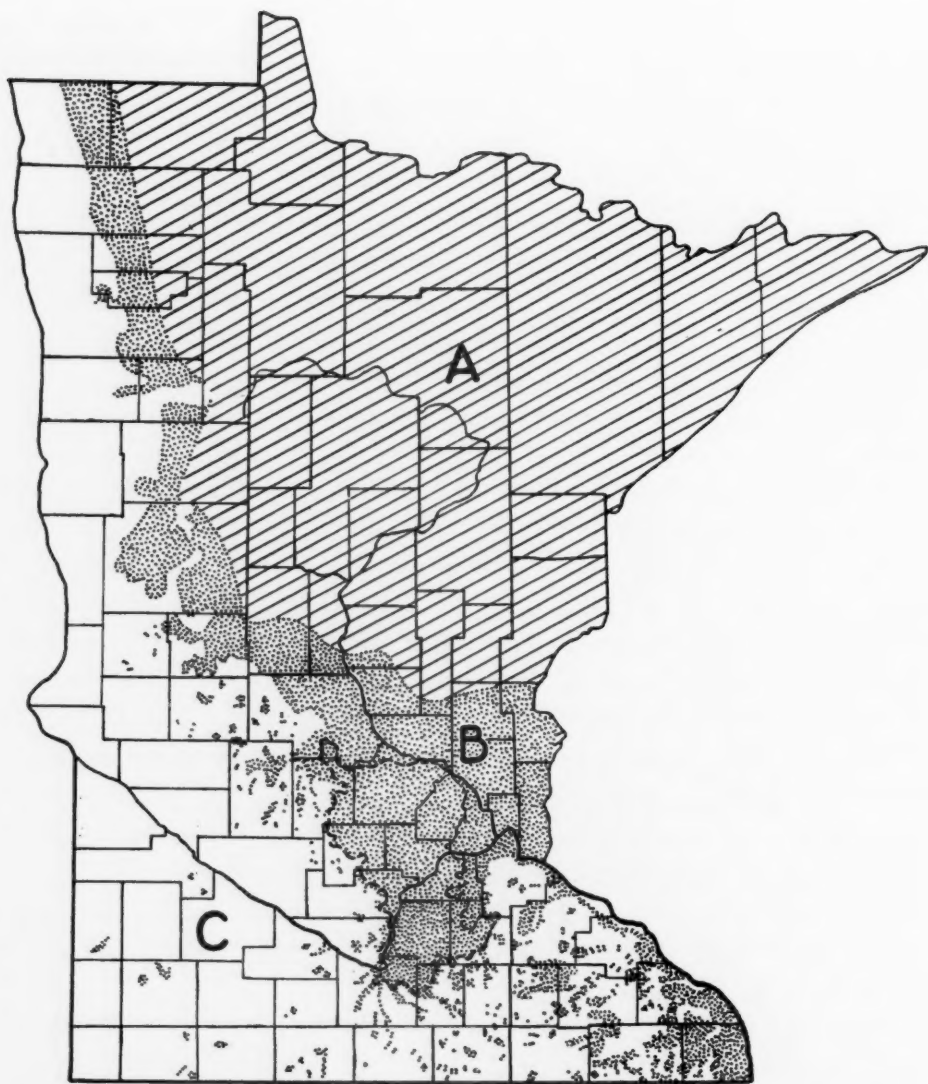


FIG. 1. Principal plant formations of Minnesota, after Upham (1884). The Big Woods is indicated by the broken line. A. Region characterized by pine subclimax communities. Climax types are sugar maple-basswood in the south and western parts, spruce-fir-birch (boreal conifer forest) in the extreme northeastern portion, and fir-basswood in the intermediate region. B. Region characterized by pure deciduous forest, with subclimax communities of oak and aspen, and sugar maple-basswood as climax. C. Region of tall-grass prairie.

SOCIOLOGY OF THE COMMUNITY

The scarcity of surviving virgin tracts of the Big Woods quite justifies a study of the original structure of the community based on these remnants before they too are destroyed. It has been possible to find and study two areas of near-virgin stands; one of these, to which I shall refer as the "Minnetonka Woods," has suffered a slight period of grazing a number of years ago,

the other, the "Northfield Woods," has been but slightly disturbed by the removal of a few trees.

QUANTITATIVE STUDIES

MINNETONKA WOODS

Two excellent remnants of the Big Woods occur on private estates located near Sunrise Point on the east side of Lake Minnetonka in Hennepin County. The home of the late R. M. Bennett is surrounded by a strip of forest, part of which from all appearances is in perfect state of preservation. Mr. Bennett stated in a letter to the writer, however, that previous to his purchase of the land in April, 1900, this forest was subjected to grazing by sheep and goats for a period which he estimated at four years. Since 1900 the forest has not been disturbed, and in this interval of thirty-five years the community has so completely recovered from the short period of disturbance that there now is no apparent evidence of the pasturing save for the persistence of a few patches of weeds (chiefly *Arctium* and *Acalypha*). A similar area of forest occurs about one-eighth mile south of the Bennett woods.

A total of 25 sets of plots was studied in these two pieces of timber at Lake Minnetonka. The locations of all quadrats were predetermined from sketch maps made for the purpose, to eliminate personal judgment in their selection. The distances between the centers of adjacent quadrats varied from 20 to 34 meters. The irregular distribution of the better patches of timber makes impossible an estimate of the total area from which the samples were taken.

Trees 1 inch d.b.h. (diameter breast high, i.e., 4.5 feet above the ground) and over were studied in 25 quadrats, each 10 meters square. In one predetermined corner of each of these larger plots was located a plot 2 x 8 meters. Trees under 1 inch d.b.h and shrubs were studied in these areas. Data concerning the forest floor herbs were derived from 4 plots, 0.25 x 4 meters each, located one in each corner of the 10 x 10 meter plots.

The rectangular or strip plots were used in preference to the usual square on the strength of investigations by Clapham (1932) and Ilvessalo (1922), which seem to indicate that by using the elongate form a smaller area is sufficient to give a true statistical picture of a community than if the square is employed. The elongate form was deemed especially desirable when dealing with the lower life forms, since such species are more frequently grouped into isodiametric 'families' which may coincide with an isodiametric plot or be entirely excluded. Obviously, an elongate plot intercepts more than one of these 'families' more often than would a square plot, and thus gives less erratic results.

Quadrat data concerning the herbs were obtained during the last two weeks of July, 1933. At this time, practically all of the withering elements of the

spring flora could still be counted and identified with ease, and the fall species were developed sufficiently so that they also could be determined by one acquainted with the flora.

TABLE 1. Density of tree species per 2,500 sq. meters, Minnetonka Woods.

| | Individuals less than 1 in. d.b.h. ² | | Individuals 1 in. d.b.h. or over | | | Totals |
|--|--|-------------------------|-------------------------------------|-------------------|--------------------------|--------|
| | 1 ft. tall or less | More than 1 ft. tall | 1-3 in. d.b.h. | 4-9 in. d.b.h. | 10 in. or more d.b.h. | |
| <i>Acer saccharum</i> Marsh..... | 12,915 | 2,453 | 102 | 28 | 25 | 15,523 |
| <i>Tilia americana</i> L..... | 33 | 17 | 17 | 6 | 16 | 89 |
| <i>Ulmus fulva</i> Michx..... | 477 ³ | 55 | 12 | 1 | 4 | 577 |
| <i>Ulmus americana</i> L..... | | 22 | 1 | 0 | 5 | |
| <i>Ostrya virginiana</i> ⁴ K. Koch. | 11 | 61 | 21 | 0 | 0 | 93 |
| <i>Quercus borealis maxima</i> Ashe | 0 | 6 | 1 | 0 | 3 | 10 |
| <i>Celtis occidentalis</i> L..... | 50 | 11 | 0 | 0 | 0 | 61 |
| Totals | 13,486 | 2,625 | 154 | 35 | 53 | 16,353 |

Density. As defined by European plant sociologists, density refers to the number of individuals of a species which occurs on a given area. Tables 1, 2, and 3 contains the results of a study of density of the sugar maple-basswood community at Lake Minnetonka.

On the basis of numbers of mature individuals, this community is quite properly called a sugar maple-basswood association. Maple reproduces prolifically by seed, and the effects of natural thinning are clearly seen in comparing the density figures from left to right. The very low density of basswood in the "seedling" stages appears even more remarkable when it is stated that even after diligent search the writer did not discover a single basswood seedling in these woods during the entire growing seasons of 1933 and 1934, nor any saplings which seemed undoubtedly of direct seedling origin. As a rule basswood seeds germinate well in this region, but apparently the seedlings become established only rarely. Once established, however, the individual seems capable of perpetuating itself indefinitely by basal sprouts. Since the sprouts of basswood have nearly as great density as the mature trees, it follows that mortality must be very low. This is a direct consequence of the manner of reproduction; the young sprouts have a more mature root system to depend upon for water, and are thus preserved during the dry seasons which take heavy toll among seedlings. Due to this type of reproduction, all basal sprouts of *Tilia* had to be considered as individuals in the plot studies. The behavior of the two most important trees in this association is thus sharply contrasted in their methods of reproduction.

The two elms illustrate an example of close ecological similarity between two species in the same genus.

² The figures in this category have been multiplied by the proper figure to compensate for the smaller sized plot used in obtaining these data.

³ These species could not always be differentiated at this stage of growth.

⁴ A small tree.

The environmental requirements of *Celtis* seem very close to those of the true climax species, but the conditions maintained in this forest evidently will not permit it to mature. The tree is characteristically a river-terrace species in this region, although I have occasionally seen mature specimens in poorly drained sites of the sugar maple-basswood forest.

TABLE 2. Density of shrub species per 100 square meters (25 plots, 2 x 8 meters each). Minnetonka Woods.

| SPECIES | No. of Plants | SPECIES | No. of Plants |
|--------------------------------------|---------------|--|---------------|
| <i>Parthenocissus vitacea</i> | | <i>Zanthoxylum americanum</i> Mill. | 16 |
| (Knerr) Greene | 147 | <i>Rhus toxicodendron</i> L. | 6 |
| <i>Celastrus scandens</i> L. | 136 | <i>Vitis vulpina</i> L. | 3 |
| <i>Sambucus pubens</i> Michx. | 28 | <i>Rubus occidentalis</i> L. | 3 |
| <i>Menispermum canadense</i> L. | 28 | | |
| <i>Ribes cynosbati</i> L. | 20 | Total | 387 |

TABLE 3. Density of herbaceous species per 100 square meters (100 plots, 0.25 x 4 meters each). Minnetonka Woods.

| SPECIES | No. of Plants | SPECIES | No. of Plants |
|--|---------------|--|---------------|
| <i>Uvularia grandiflora</i> Sm. | 812 | <i>Arenaria lateriflora</i> L. | 17 |
| <i>Osmorhiza claytoni</i> | | <i>Arisaema triphyllum</i> (L.) Schott. .. | 13 |
| (Mich.) Clarke. | 728 | <i>Botrychium virginianum</i> (L.) Sw. .. | 13 |
| <i>Circaea lutetiana</i> L. | 377 | <i>Actaea rubra</i> (Ait.) Willd. | 11 |
| <i>Solidago latifolia</i> L. | 215 | <i>Aralia nudicaulis</i> L. | 10 |
| <i>Viola pubescens</i> Ait. | 157 | <i>Desmodium grandiflorum</i> | |
| <i>Carex pennsylvanica</i> Lam. | 148 | (Walt.) DC. | 10 |
| <i>Sanguinaria canadensis</i> L. | 141 | <i>Sanicula gregaria</i> Bicknell. | 9 |
| <i>Amphicarpa pitcheri</i> T. & G. | 115 | <i>Cryptotaenia canadensis</i> (L.) DC. ... | 7 |
| <i>Maianthemum canadense</i> Desf. | 61 | <i>Caulophyllum thalictroides</i> | |
| <i>Smilacina racemosa</i> (L.) Desf. | 53 | (L.) Michx. | 5 |
| <i>Thalictrum dioicum</i> L. | 46 | <i>Carex laxiflora latifolia</i> Boott. | 4 |
| <i>Laportea canadensis</i> (L.) Gaud. | 45 | <i>Smilax herbacea</i> L. | 4 |
| <i>Phryma leptostachya</i> L. | 42 | <i>Ranunculus abortivus</i> L. | 3 |
| <i>Hydrophyllum virginianum</i> L. | 36 | <i>Asplenium filix-femina</i> (L.) Bernh. 2 | |
| <i>Galium triflorum</i> Michx. | 33 | <i>Geranium maculatum</i> L. | 1 |
| <i>Polygonatum biflorum</i> (Walt.) Ell. 31 | | | |
| <i>Alliaria officinalis</i> ⁵ Andrz. | 27 | Total | 3,081 |

Close scrutiny of the quadrat data shows no irregularity which might be taken as evidence of the period of disturbance by grazing which was mentioned previously. Among the several influences which a period of grazing should have had on the forest would be that the seedlings of the trees during these years, together with small trees only a few years old, would have been eaten or trampled, and thus greatly reduced in numbers. Furthermore, as time went on, there would always be one size class represented by a paucity of individuals, and this group would move progressively through the higher classes to the mature size and then be obliterated. A curve based on all indi-

⁵ This herb is a weed introduced into eastern North America from Europe.

vidual maples in the quadrats, separating the diameter classes into 1-inch intervals, shows a smooth gradual decline with increasing size, which is suggestive of an uninterrupted process of natural thinning. If the grazing had been severe, or of long duration, there should now be an abrupt break in such a curve occurring somewhere about the 5-inch diameter class.

Frequency. In current phytosociological usage, the term frequency is employed to designate the percentage of quadrats, of the total number examined, in which a species occurs. Tables 4, 5, and 6 contain the frequency percentage for all of the vascular plants which occurred in the plots.

TABLE 4. Frequency of the tree species. Minnetonka Woods.

| | Individuals less than 1 in. d.b.h. ⁶ | | | Individuals 1 in. d.b.h. or over ⁷ | |
|--------------------------------------|--|-------------------------|-------------------|--|--------------------------|
| | 1 ft. tall or less | more than 1 ft. tall | 1-3 in. d.b.h. | 4-9 in. d.b.h. | 10 in. or more d.b.h. |
| <i>Acer saccharum</i> | 100% | 100 | 80 | 60 | 76 |
| <i>Tilia americana</i> | 4 | 4 | 36 | 16 | 48 |
| <i>Ulmus fulva</i> | | 32 | 24 | 4 | 16 |
| <i>Ulmus americana</i> | 64 ⁸ | 8 | 4 | 0 | 20 |
| <i>Quercus borealis maxima</i> | 0 | 4 | 4 | 0 | 8 |
| <i>Ostrya virginiana</i> | 8 | 12 | 28 | 0 | 0 |
| <i>Celtis occidentalis</i> | 16 | 8 | 0 | 0 | 0 |

The predominance of sugar maple is again attested by its high frequency. The sequence of importance among the trees is approximately the same in frequency as in density. The very low frequency of *Tilia* in the smaller size classes reflects the clustered nature of the basal sprouts.

TABLE 5. Frequency of shrub species (25 plots, 2 x 8 meters each). Minnetonka Woods.

| SPECIES | Per Cent | SPECIES | Per Cent |
|-------------------------------------|----------|-------------------------------------|----------|
| <i>Parthenocissus vitacea</i> | 68 | <i>Vitis vulpina</i> | 12 |
| <i>Sambucus pubens</i> | 48 | <i>Zanthoxylum americanum</i> | 4 |
| <i>Ribes cynosbati</i> | 32 | <i>Rhus toxicodendron</i> | 4 |
| <i>Celastrus scandens</i> | 16 | <i>Rubus occidentalis</i> | 4 |
| <i>Menispermum canadense</i> | 12 | | |

Among the shrubs, *Celastrus* has a very high density, while its frequency rating is relative much lower. This signifies many individuals distributed in groups over the forest. Such a distribution, referred to as "hyperdisperse" by Schustler (see Braun-Blanquet 1932, p. 31), is obvious to anyone who would make even a superficial survey of the forest, yet it is only by the comparison of studies of density and frequency that such a condition can be expressed in tangible form.

Sambucus, by way of contrast, is quite high in frequency and comparatively low in density. Accordingly, the few plants are found well scattered over the forest floor. Schustler refers to this type of distribution as "hypo-disperse."

⁶ Data derived from 25 plots, 2 x 8 meters each.

⁷ Data derived from 25 plots, 10 x 10 meters each.

⁸ These species could not always be differentiated at this stage of growth.

TABLE 6. Frequency of herbaceous species (100 plots, 0.25 x 1 meter each).
Minnetonka Woods.

| SPECIES | Per Cent | SPECIES | Per Cent |
|---------------------------------------|----------|---|----------|
| <i>Osmorhiza claytoni</i> | 83 | <i>Arisaema triphyllum</i> | 6 |
| <i>Utricularia grandiflora</i> | 64 | <i>Laportea canadensis</i> | 6 |
| <i>Circaea lutetiana</i> | 49 | <i>Sanicula gregaria</i> | 4 |
| <i>Viola pubescens</i> | 45 | <i>Caulophyllum thalictroides</i> | 4 |
| <i>Sanguinaria canadensis</i> | 41 | <i>Carex laxiflora latifolia</i> | 3 |
| <i>Amphicarpa pitcheri</i> | 25 | <i>Desmodium grandiflorum</i> | 3 |
| <i>Thalictrum dioicum</i> | 25 | <i>Smilax herbacea</i> | 3 |
| <i>Phryma leptostachya</i> | 23 | <i>Arenaria lateriflora</i> | 2 |
| <i>Carex pennsylvanica</i> | 19 | <i>Alliaria officinalis</i> | 2 |
| <i>Smilacina racemosa</i> | 16 | <i>Cryptotaenia canadensis</i> | 2 |
| <i>Maianthemum canadense</i> | 13 | <i>Ranunculus abortivus</i> | 2 |
| <i>Hydrophyllum virginianum</i> | 11 | <i>Aralia nudicaulis</i> | 2 |
| <i>Polygonatum biflorum</i> | 11 | <i>Actaea rubra</i> | 2 |
| <i>Galium triflorum</i> | 10 | <i>Geranium maculatum</i> | 1 |
| <i>Solidago latifolia</i> | 10 | <i>Asplenium filix-femina</i> | 1 |
| <i>Botrychium virginianum</i> | 9 | | |

The most important members of the herbaceous flora are not confined to any one seasonal aspect. *Utricularia*, *Viola* and *Sanguinaria* flower in spring, *Circaea* and *Osmorhiza* in summer, and *Solidago* is a characteristic autumnal plant. The last species presents another good example of the hyperdisperse type of distribution, being high in density and low in frequency.

Dominance. Basal area was computed as a measure of relative dominance among the tree species. This analysis is made by converting the diameter breast high into cross-sectional area for each individual 1 inch d.b.h. or over, and then adding up all the individual areas for each species. Table 7 shows the preponderant importance of *Acer*, with *Tilia* again second in importance. As in the preceeding studies, the elms are third in importance and the red oak last.

TABLE 7. Basal area of tree species in square feet, per 2,500 square meters, individuals smaller than 1 inch d.b.h. are excluded. Minnetonka Woods.

| SPECIES | 1-3 inches d.b.h. | 4-9 inches d.b.h. | 10 inches or more d.b.h. | Total |
|--------------------------------------|----------------------|----------------------|-----------------------------|----------|
| <i>Acer saccharum</i> | 1.5544 | 5.5143 | 44.2409 | 51.3096 |
| <i>Tilia americana</i> | .3710 | 1.2055 | 26.8510 | 28.4275 |
| <i>Ulmus americana</i> | .0055 | .0000 | 9.9797 | 9.9855 |
| <i>Ulmus fulva</i> | .1582 | .2673 | 6.6649 | 7.0904 |
| <i>Quercus borealis maxima</i> | .0490 | .0000 | 6.1414 | 6.1904 |
| <i>Ostrya virginiana</i> | .3353 | .0000 | .0000 | .3353 |
| Total | 2.4734 | 6.9871 | 93.8779 | 103.3387 |

A record of the maximum diameters of the tree species is worthy of inclusion at this point. The following figures represent the d.b.h. of the largest specimens of the species which the writer found on the uplands within the Big Woods region:

| | Inches | | Inches |
|------------------------------|--------|--------------------------------------|--------|
| <i>Acer saccharum</i> | 29 | <i>Ulmus fulva</i> | 20 |
| <i>Tilia americana</i> | 30 | <i>Quercus borealis maxima</i> | 32 |
| <i>Ulmus americana</i> | 41 | <i>Ostrya virginiana</i> | 9 |

The elms in particular attain much larger size with an approach toward poorly drained conditions. In such a habitat I measured one American elm which had a d.b.h of 6 feet 3 inches.

Phytographs have been constructed for the tree species of the Minnetonka Woods. This type of diagram, devised by Lutz (1930), is intended to portray graphically the relative importance of the species.

The larger the area of the trapezium (Fig. 2), the more important the species in the community. The lower radius (No. 3) is very critical as an indicator of the reproductive success of the species. If a species is represented in the plots by all five size classes, the lower angle of the trapezium extends to the edge of the circle. When any one size class is lacking, the trapezium ends four-fifths of the distance to the circle. One serious criticism of this method of showing size classes is that it does not indicate *which* of the classes is absent. An example which illustrates this weakness is as follows: In the Northfield Woods, *Carya cordiformis* K. Koch. reproduces successfully but does not attain a diameter sufficient to give it a place in the largest size class (Table 8), in spite of the fact that it is mature from the reproductive standpoint and is a member of the dominant stratum. A phyto-graph of this species would show the presence of only four size classes and give the impression that it is not a climax tree. It is important to know whether it is the largest size class, intermediate, or the smallest one which is not represented in the forest.

The first three of the species shown in the phyto-graph are apparently stable. The same is true of *Ostrya*; the poor representation in the phyto-graph reflects the limited size of the mature trees. *Ulmus fulva* and the oak, according to the diagram, do not appear to be reproducing successfully, but such is not the case. For these species, which have low density but also low mortality, the number of plots studied covered an area insufficient to include all size classes.

Floristic list of the Minnetonka Woods. An attempt was made to compile a complete species list of all the trees, shrubs, and herbs which occur in the least-disturbed parts of this forest. Aside from those recorded in the plots, no additional tree species were found, and only one shrub, *Prunus virginiana* L., can be added to the shrub list. Among the herbs, the following list should be added to the group for which density and frequency have been given: *Allium tricoccum* Ait., *Anemone quinquefolia* L., *Aplectrum hyemale* (Muhl.) Torr., *Aquilegia canadensis* L., *Aralia racemosa* L., *Eupatorium urticaefolium* Reichard., *Galium aparine* L., *Hepatica acutiloba* DC., *Panax quinquefolium* L., *Sanicula marilandica* L., *Trillium cernuum* L., *Viola canadensis* L.

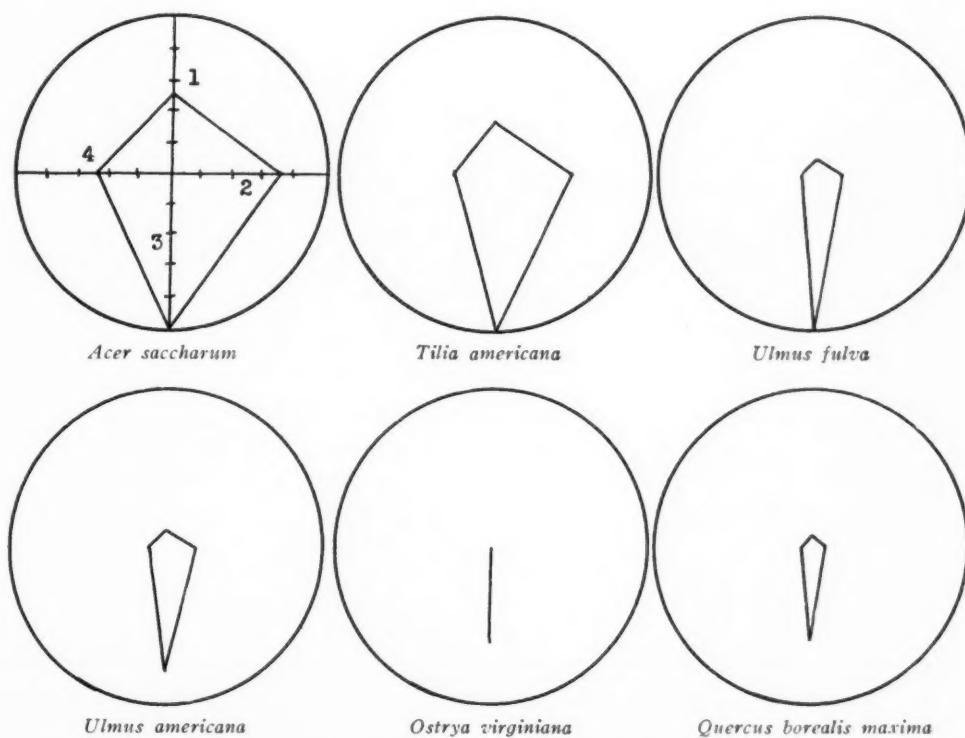


FIG. 2. Phytographs of the tree species in the Minnetonka Woods. The inner end of each radius represents 0 for each of the 4 sociological characteristics:

Radius 1. Density:⁹ each species representing a percentage of the total density of stems 10 inches d.b.h. and over.

Radius 2. Frequency: percentage of the 25 quadrats (10 x 10 meters) in which stems 10 inches d.b.h. or over occurred.

Radius 3. Size classes: number of size classes, as separated in Table 1, by which the species is represented.

Radius 4. Dominance (as measured by basal area): each species represented as a percentage of the total basal area of all stems 10 inches d.b.h. and over which occurred in the quadrats.

The figures for which the phytograph for Acer is based, for example, are: density 47 per cent, frequency 76 per cent, size classes 5, basal area 47 per cent.

NORTHFIELD WOODS

In making reconnaissance surveys of many isolated stands of the Big Woods, it became apparent that while quite a number of stands seem to have once been identical in composition with the Minnetonka Woods, others differed in having a wider variety of tree species. The Northfield Woods seemed quite representative of this richer type of community and since it seemed to be the least cut over of the ungrazed remnants, it was chosen for special study. The stand is located in Rice County just opposite the southwest corner of Dakota County, approximately 35 miles south-southeast of the Minnetonka Woods (see location in Fig. 4).

⁹ In the original description of the phytograph, Lutz did not differentiate between "density" which is statistically exact, and "abundance" which is an estimate of density. Apparently he used density data and referred to them as "abundance."

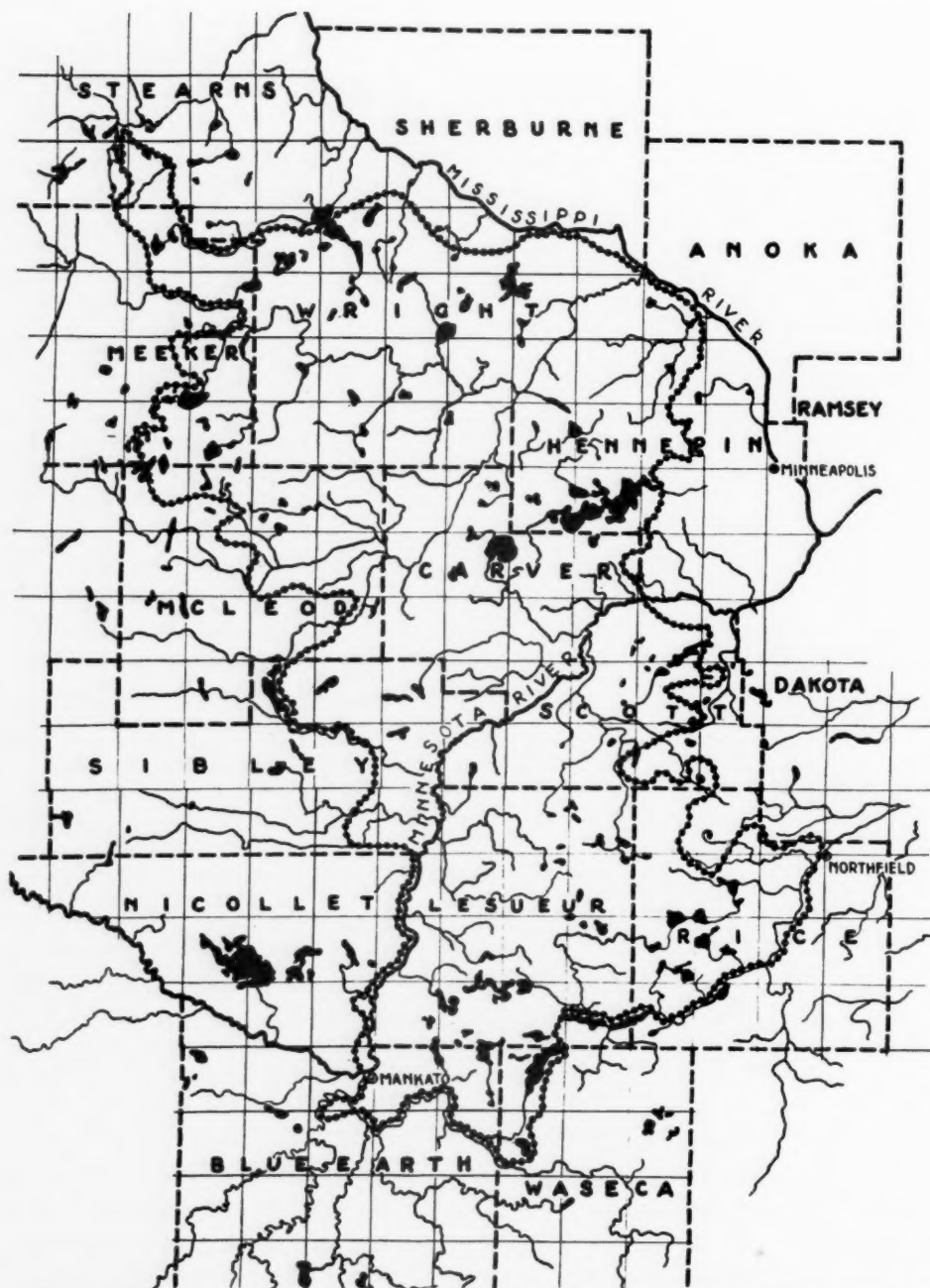


FIG. 3. Detailed map of the Big Woods showing the relation of certain parts of the forest boundaries to lakes and streams.

In the summer of 1934, twenty-five 10 x 10 meter quadrats were studied, together with an equal number of 2 x 8 meter areas. Only the tree species were considered. The data have been analyzed so that tables for density, frequency, and basal area (Tables 8, 9, and 10) are directly comparable to those concerning the Minnetonka Woods.

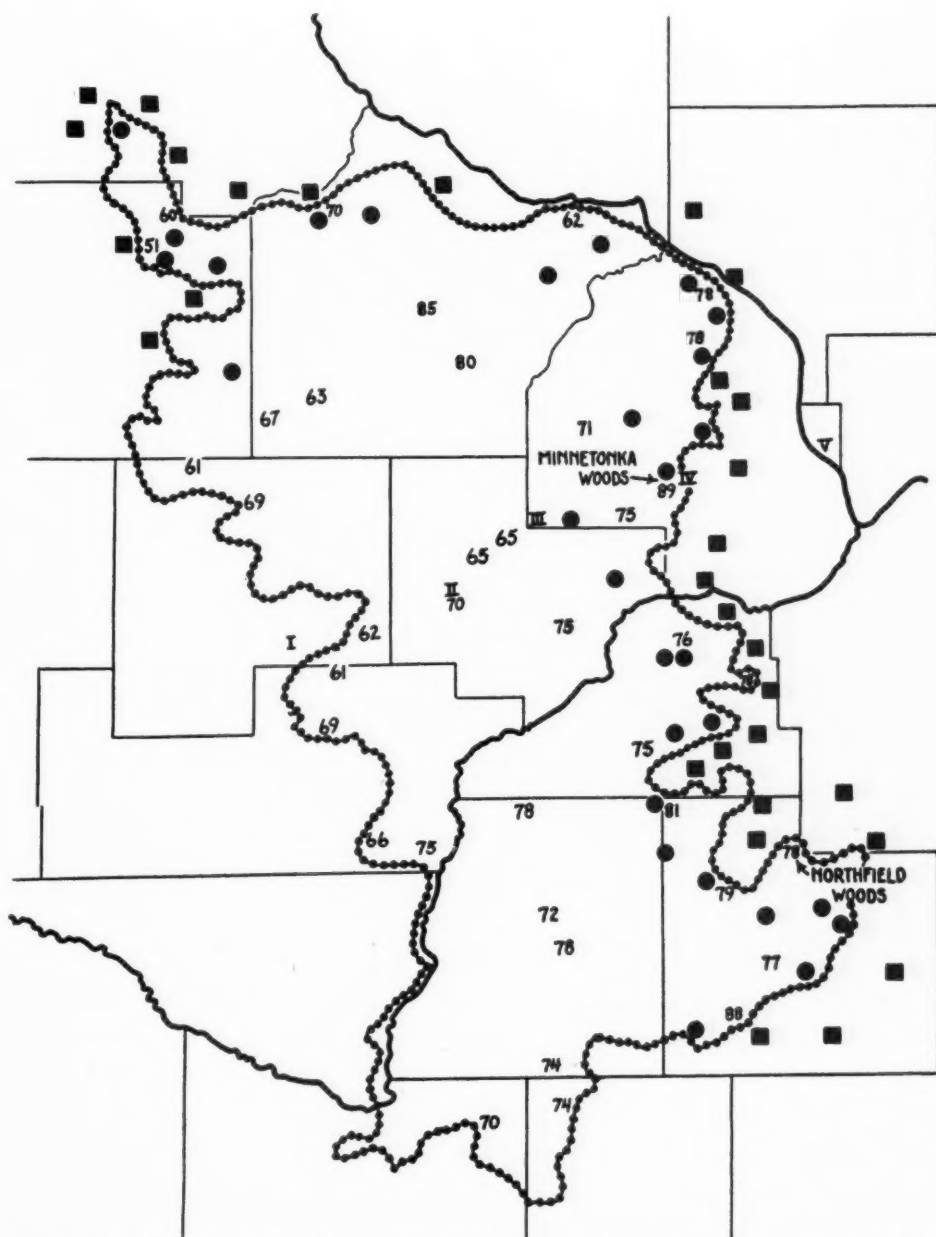


FIG. 4. Outline map of the Big Woods showing location of forest height measurements, the 5 climatological stations (indicated by Roman numerals), the Minnetonka and Northfield Woods, and the stations where soils were tested in the Mixed Oak Forest (indicated by squares) and in the Big Woods (indicated by circles).

Several marked differences are apparent when the data for the two forests are compared. The six tree species which complete the list of the Minnetonka community are also the principal dominants of the Northfield Woods, but they are accompanied by *Fraxinus pennsylvanica*, *F. pennsylvanica lanceolata*, *Carya cordiformis*, and *Quercus macrocarpa olivaceiformis*. According to the

plot data, *Acer negundo* germinates but does not mature here—a parallel to the behavior of *Celtis* at Lake Minnetonka. Bur oak, with only one seedling and no intermediate sizes, is definitely not a member of the climax community in the strict sense, but probably owes its existence to local openings in the forest which occasionally permit the species to gain a foothold. Aside from the species recorded in the plots, *Juglans cinerea* L. also occurs here. This piece of timber, then, is dominated by the same species, and in nearly the same proportion, which compose the Minnetonka Woods, but has in addition four other species which seem to be integral parts of the mature community.

TABLE 8. Density of tree species per 2,500 square meters. Northfield Woods.

| | Individuals less than 1 in. d.b.h. ¹⁰ | | 1-3 in. d.b.h. | Individuals 1 in. d.b.h. or over | | Totals |
|---|---|-------------------------|-------------------|-------------------------------------|--------------------------|--------|
| | 1 ft. tall or less | more than 1 ft. tall | | 4-9 in. d.b.h. | 10 in. or more d.b.h. | |
| <i>Acer saccharum</i> | 400 | 837 | 58 | 46 | 15 | 1,356 |
| <i>Tilia americana</i> | 0 | 19 | 1 | 8 | 26 | 54 |
| <i>Quercus borealis maxima</i> | 31 | 0 | 0 | 3 | 12 | 46 |
| <i>Ulmus americana</i> | 131 ¹¹ | 6 | 5 | 1 | 6 | 230 |
| <i>Ulmus fulva</i> | | 75 | 3 | 3 | 0 | |
| <i>Ostrya virginiana</i> | 0 | 0 | 11 | 4 | 0 | 15 |
| <i>Fraxinus pennsylvanica</i> <i>lanceolata</i> Sarg. | 31 | 144 | 1 | 1 | 2 | 179 |
| <i>Fraxinus pennsylvanica</i> Marsh. | 0 | 12 | 0 | 0 | 1 | 13 |
| <i>Carya cordiformis</i> | 444 | 31 | 2 | 3 | 0 | 480 |
| <i>Quercus macrocarpa</i> <i>olivaceformis</i> Gray. | 6 | 0 | 0 | 0 | 1 | 7 |
| <i>Acer negundo</i> L. | 6 | 12 | 0 | 0 | 0 | 18 |
| Totals | 1,049 | 1,136 | 81 | 69 | 63 | 2,398 |

TABLE 9. Frequency of tree species. Northfield Woods.

| | Individuals less than 1 in. d.b.h. ¹² | | 1-3 in. d.b.h. | Individuals 1 in. d.b.h. or over ¹³ | |
|---|---|-------------------------|-------------------|---|--------------------------|
| | 1 ft. tall or less | more than 1 ft. tall | | 4-9 in. d.b.h. | 10 in. or more d.b.h. |
| <i>Acer saccharum</i> | 56 | 96 | 72 | 72 | 48 |
| <i>Tilia americana</i> | 0 | 4 | 4 | 24 | 52 |
| <i>Quercus borealis maxima</i> | 20 | 0 | 0 | 12 | 36 |
| <i>Ulmus americana</i> | 32 ¹⁴ | 4 | 12 | 4 | 24 |
| <i>Ulmus fulva</i> | | 20 | 16 | 8 | 0 |
| <i>Ostrya virginiana</i> | 0 | 0 | 20 | 8 | 0 |
| <i>Fraxinus pennsylvanica lanceolata</i> | 20 | 44 | 4 | 4 | 8 |
| <i>Fraxinus pennsylvanica</i> | 0 | 8 | 0 | 0 | 4 |
| <i>Carya cordiformis</i> | 68 | 16 | 8 | 8 | 0 |
| <i>Quercus macrocarpa olivaceformis</i> | 4 | 0 | 0 | 0 | 4 |

¹⁰ The figures in this category have been multiplied by the proper figure to compensate for the smaller size plot used in obtaining these data.

¹¹ These species could not always be differentiated at this stage of growth.

¹² Data derived from 25 plots, 2 x 8 meters each.

¹³ Data derived from 25 plots, 10 x 10 meters each.

¹⁴ These species could not always be differentiated at this stage of growth.

TABLE 10. Basal area of tree species in square feet per 2,500 square meters. Individuals smaller than 1 inch are excluded. Northfield Woods.

| | 1-3 in. d.b.h. | 4-9 in. d.b.h. | 10 in. d.b.h. or over | Totals |
|--|-------------------|-------------------|--------------------------|--------|
| <i>Acer saccharum</i> | 1.77 | 9.01 | 14.41 | 25.19 |
| <i>Tilia americana</i> | .01 | 2.10 | 50.19 | 52.30 |
| <i>Quercus borealis maxima</i> | .00 | .67 | 19.24 | 19.91 |
| <i>Ulmus americana</i> | .12 | .44 | 7.48 | 8.04 |
| <i>Ulmus fulva</i> | .03 | .71 | .00 | .74 |
| <i>Ostrya virginiana</i> | .36 | .38 | .00 | .74 |
| <i>Fraxinus pennsylvanica lanceolata</i> | .02 | .09 | 4.82 | 4.93 |
| <i>Fraxinus pennsylvanica</i> | .00 | .00 | 1.07 | 1.07 |
| <i>Quercus macrocarpa olivaeformis</i> | .00 | .00 | 1.77 | 1.77 |
| <i>Carya cordiformis</i> | .04 | .53 | .00 | .57 |
| Totals | 2.35 | 13.93 | 98.98 | 115.26 |

A second comparison concerns the reversal of the relative importance of *Tilia* and *Acer* in certain size classes. In the two larger size classes, *Tilia* is conspicuously the more important in density, frequency and dominance. However, since the maple predominates in all the other size classes, and since no maples occurred over 18 in. d.b.h. (while basswoods were found ranging up to 30 in.) it seems quite probable that the maple has at some time been disturbed either by selective cutting, or possibly injured by use in making maple sugar. There are stumps in the forest, and some of them are quite large, so that selective cutting alone might account for this paucity of large maples.

A third conspicuous feature of this forest is the relative scarcity of very young reproduction. The second size class (over 1 foot tall, yet under 1 inch d.b.h.) is better represented than the seedling stage in the maple, ashes, and box elder. This suggests that some factor may have recently interfered with the germination and establishment of seedlings. Perhaps the unusually severe drought of the latter part of May 1934, was responsible for much of this destruction of seedlings. The atmometric evaporation for this critical period within the Minnetonka Woods was exceedingly high, and must have been fatal to a large percentage of seedlings. Atmometers 1.5 meters above the forest floor lost 891 cc. from May 19 to June 2, whereas the average loss for equal periods during the remainder of the growing season was 296 cc. For this unusual period evaporation was higher within this mesic forest than it usually is on the open prairie immediately west of the Big Woods.

The total basal area of the Northfield Woods is a little greater than that of the Minnetonka Woods in spite of the cutting in the former.

This comparative study of the two samples of the Big Woods shows that even though the composition of the sugar maple-basswood community varies, six species are usually the most important, and bear the same approximate relationships to each other. Extensive but more superficial studies over the entire area further substantiate this conclusion.



FIG. 5. Minnetonka Woods in winter aspect.



FIG. 6. A large bur oak surrounded by young sprout forest composed chiefly of basswood and ironwood. Hennepin County, Minn.

While working in the Northfield Woods, the writer on several occasions noticed a tendency toward layering in both sugar maple and slippery elm (*Ulmus fulva*)—species in which the habit has not, to the writer's knowledge, been previously reported. A specimen of the maple which I preserved may be described as follows: A slender branch, originating from the base of a maple 4 inches d.b.h., about 2 cm. above the ground line, ran horizontally just beneath the litter and duff for 3 dm. and then forked. One division extended 1 dm. and the other 2 dm. further, then both turned erect. In addition, there were two other erect branches arising from the horizontal shoot at a point 1.5 dm. from its base. Roots were produced abundantly from the lower side of the prostrate stem, but only on the longer of the two creeping branches. A similar case was found in the elm, except that here the prostrate branch had arisen from a smaller parent, the aerial portions of which had in the meantime died.

QUALITATIVE ANALYSES (MINNETONKA WOODS)

Periodicity. During the growing season of 1934, the Minnetonka Woods was visited repeatedly at intervals seldom exceeding 2 weeks for the purpose of taking phenological notes.

Leaf buds of the trees were opening on April 29, and at the same time the first herbs (*Sanguinaria* and *Hepatica*) were found in bloom. Approximately 3 weeks were required for the completion of the canopy, which remained fully complete for about 15 weeks of the summer. On September 14 the leaves began to drop, and flowering among the herbs likewise ceased at about this time. By October 6 the trees were again bare.

A study of the periodicity among the herbaceous species over the entire year brings out some striking diversities within the group. The species may be classified into 15 behavior types with respect to periods of vegetative activity, flowering activity, and rest (Table 11).

Seven of the species have leaves which persist through the winter. Such leaves resemble the usual deciduous types, and are not to be classified with xeromorphic evergreen leaf types. They are almost entirely contained within the litter, and get additional protection from the more or less continuous covering of snow in winter.

All herbs flower between the time when the foliar buds of the trees burst, and when the leaves begin to drop in the fall. All of the tree species except basswood are anemophilous and come into flower either before the canopy begins to develop, or at the latest, before it is completely developed. *Tilia* blossoms about a month after the canopy is fully developed (first week in June, 1934).

Stratification. The plants of the Minnetonka Woods may be grouped into 6 strata: 1. moss, 2. low herb, 3. tall herb-low shrub, 4. tall shrub, 5. small

tree, 6. dominant tree. The moss stratum is restricted to bare areas formed by material brought to the surface by woodchucks, or exposed by windthrown trees. A group of eight species 2 to 6 inches tall constitute a scattered and poorly defined low-herb stratum. Eighty per cent of the herbaceous species attain a height of 7 to 14 inches. The distinctness of this sub-community is accentuated by the inclusion of three shrub species (*Parthenocissus*, *Celastrus*, and *Rhus*), which include 75 per cent of all the shrubby individuals of the forest. A separate stratum of taller shrubs is very inconspicuous. A fifth stratum of low trees includes only one species, *Ostrya virginiana*. Thus only two strata—the dominant trees and the tall herb-low shrub group—stand

TABLE 11. Periodicity of herbs, Minnetonka Woods. Explanation of symbols: L = apparently functional leaves present; F = flowering; * = no living aerial shoots, or at most very immature shoots. *Winter* is defined as: the months of severest cold (December, January and February) and most of March and April; *Spring*: interval from the time of opening of leaf buds of trees to the time when the canopy is fully developed (approximately the first three weeks of the growing season; *Summer*: period of complete canopy; *Fall*: period between the inception of leaf fall and winter.

| Behavior Types | Examples | Winter | Spring | Seasons early | Summer mid. | late | Fall |
|-------------------|--|--------|--------|------------------|----------------|------|------|
| 1. | <i>Carex pennsylvanica</i> , <i>C. laxiflora latifolia</i> , <i>Galium triflorum</i> , <i>Hepatica acutiloba</i> <i>Ranunculus abortivus</i> | L | LF | L | L | L | L |
| 2. | <i>Osmorhiza claytoni</i> | L | L | LF | L | L | L |
| 3. | <i>Galium aparine</i> <i>Actaea rubra</i> , <i>Anemone</i> <i>quinquefolia</i> , <i>Aralia nudicaulis</i> | * | LF | L | * | * | * |
| 4. | <i>Caulophyllum thalictroides</i> , <i>Thalictrum</i> <i>dioicum</i> , <i>Trillium cernuum</i> , <i>Urtularia</i> <i>grandiflora</i> , <i>Viola pubescens</i> | * | LF | L | L | L | * |
| 5. | <i>Aquilegia canadense</i> | * | LF | LF | L | * | * |
| 6. | <i>Sanguinaria officinalis</i> | * | LF | L | L | L | * |
| 7. | <i>Aplectrum hyemale</i> | L | L | F | * | * | L |
| 8. | <i>Allium tricoccum</i> | * | L | F | * | * | * |
| 9. | <i>Arenaria latiflora</i> , <i>Geranium maculatum</i> , <i>Laportea canadensis</i> , <i>Polygonatum</i> <i>biflorum</i> , <i>Smilacina racemosa</i> | * | L | LF | L | L | L |
| 10. | <i>Arisaema triphyllum</i> | * | LF | LF | L | * | * |
| 11. | <i>Hydrophyllum virginianum</i> | * | L | LF | L | L | L |
| 12. | <i>Aralia racemosa</i> , <i>Cryptotaenia</i> <i>canadense</i> , <i>Panax quinquefolia</i> , <i>Sanicula</i> <i>gregaria</i> , <i>S. marilandica</i> , <i>Smilax</i> <i>herbacea</i> | * | * | LF | L | L | * |
| 13. | <i>Amphicarpa pitcheri</i> , <i>Circaea</i> , <i>Desmodium grandiflorum</i> , <i>Phryma leptostachya</i> | * | * | L | LF | L | * |
| 14. | <i>Solidago latifolia</i> , <i>Eupatorium</i> <i>urticaefolium</i> | * | * | L | L | LF | * |
| 15. | <i>Alliaria officinalis</i> | * | * | LF | LF | L | L |

out distinctly. The others are exceedingly poor in species and in individuals and, further, the structure is masked by the complete series of transgressive individuals which form the reproduction of the dominant stratum.

Life forms. A classification of the species of the Minnetonka Woods according to Raunkiaer's life form system (Smith 1913) is presented in Table 12. While this scheme was originally intended for use on a larger scale, i.e. to be applied to the complete floristic list of all habitats of a region, it may also be used to advantage in comparing community types.

TABLE 12. Life form classification of the species of the Minnetonka Woods.

| | Size Class | No. of spp. | Percentage |
|-------------------|------------|-------------|------------|
| Mesophanerophyte | | 6 | 10 |
| Microphanerophyte | | 2 | 3 |
| Nanophanerophyte | | 5 | 9 |
| Chamaephyte | | 8 | 14 |
| Hemicryptophyte | | 17 | 29 |
| Geophyte | | 19 | 33 |
| Therophyte | | 1 | 2 |
| Totals | | 58 | 100 |

The community is evidently a forest dominated by mesophanerophytes, with an undergrowth composed chiefly of geophytes and hemicryptophytes.

Leaf-size classes. A classification of the vascular plants of the Minnetonka Woods, according to Raunkiaer's system of leaf size classes (Fuller and Bakke 1918) is presented in Table 13.

TABLE 13. Leaf-size classes of the vascular species of the Minnetonka Woods. (In compound leaves, the leaflet is taken as the unit; all of the plants have deciduous leaves.)

| | Classification | Herbs | Shrubs | Trees | Totals |
|----------|----------------|-------|--------|-------|--------|
| Simple | Mesophyll | 15 | 3 | 6 | 24 |
| | Microphyll | 5 | 2 | 0 | 7 |
| | Nanophyll | 4 | 0 | 0 | 4 |
| Compound | Mesophyll | 4 | 2 | 0 | 6 |
| | Microphyll | 11 | 3 | 0 | 14 |
| | Nanophyll | 3 | 0 | 0 | 3 |
| Totals | | 42 | 10 | 6 | 58 |

Of the 58 species, 63 per cent (35) have simple leaves. Among the simple leaves, mesophylls, predominate, but in the compound-leaf group, microphylls are most important. Raunkiaer's smallest class (leptophyll) and two largest (macro- and megaphyll) are not represented in this forest. The leaves of the dominant stratum are all simple deciduous mesophylls.

Perhaps a better way of expressing the relative importance of the different leaf size classes (or life form classes either, for that matter) is by adding up the absolute densities of all species of similar leaf size. Such a summation expresses the total number of individuals, regardless of species, in each leaf size-class. This method is not floristic but physiognomic, and has more biolog-

ical significance and descriptive value than the use of simple floristic list. In Table 14 the scheme has been carried out for all species which occurred in the quadrats at Lake Minnetonka; consequently, the list of species considered is not quite so large as that used in the above table.

TABLE 14. Leaf-size classes, based on density figures of each major life form. In compound leaves, the leaflet is taken as the unit. Leaflets of compound leaves have been lumped with the simple leaves of the same size class.

| Life Form | Leaf-size Class | Total Individuals per 100 sq.m. |
|-----------|------------------|------------------------------------|
| Tree | mesophyll | 2.5 |
| | mesophyll | 80.0 |
| Shrub | microphyll | 16.7 |
| | mesophyll | 1129.0 |
| Herb | microphyll | 1788.0 |
| | nanophyll | 259.0 |

This method gives a picture of the forest somewhat different from that furnished by the one generally used. According to the above table, over 80 per cent of the shrubby plants are mesophylls and comparatively few are microphylls, but judging from the method of Table 13, mesophylls and microphylls are of equal importance. Similarly, Table 14 indicates that microphyllous herbs are more numerous as individuals than are mesophyllous herbs, which is the reverse of the condition as indicated by the simple floristic method.

Lianas. One herbaceous liana (*Amphicarpa pitcheri*) is moderately abundant, but the species under average crown density is usually a straggling plant. In openings the plant climbs a few meters high. *Menispermum canadense* attains a height of several meters but the parts of the stem not protected by litter are killed each winter. The same tendency for the persisting portions of the stem to occur chiefly under the litter and duff is shown by *Parthenocissus vitacea* and *Rhus toxicodendron*. Both of these have prostrate stems with upright branches about 1 dm. tall in the case of the former, and 2 dm. in the latter. The plants may best be characterized as potential lianas. On river bottoms, both climb to considerable height. In the Big Woods *Parthenocissus* sometimes climbs a meter or two, but *Rhus* never. *Celastrus scandens* occurs as a straggling shrub under average canopy density, but where the forest is more open, it climbs to 2 meters or more. It fruits only under the latter conditions. *Vitis vulpina* is a woody liana commonly attaining a height of several meters.

Epiphytes. Epiphytes are poorly represented in the Big Woods. Mosses are common in patches on the bases of large trees. Usually these are confined to the lower 3 dm. of the trunk, but occasionally may extend up as much as 3 meters. A species of *Porella* is often mixed with the mosses around the bases of the trees. Crustose lichens are common on the smaller boughs near the top of the tree canopy.

BOUNDARIES OF THE BIG WOODS

SURROUNDING VEGETATION

To the west and south of the Big Woods, the original vegetation seems to have been either bur oak savanna or tall-grass prairie. Transitions between the sugar maple-basswood forest and these communities were apparently sharp as a rule, yet instances are not rare where a distinct gradation existed from pure sugar maple-basswood through a mixture of this community with bur oak, to pure bur oak forest and savanna. Prairie and Big Woods transitions are not common, and where they exist they are always sharp.

Beginning near the northwest corner of the Big Woods and extending around the northern and eastern edges of this forest, the adjacent vegetation may be characterized as a mixed oak forest. The species involved are: *Quercus ellipsoidalis*, *Q. macrocarpa olivaeformis*, *Q. alba*, *Q. coccinea* (extending no farther north than Minneapolis), *Q. borealis maxima*, and *Ostrya virginiana*. The last three are much less common than the first three. *Quercus borealis maxima* and *Ostrya* have the most mesic requirements, and are chiefly confined to shaded slopes. Any of the three most abundant species may occur as a fairly pure stand. All sorts of combinations are found grading to a complete mixture of the entire series. This forest is obviously a more xeric community than the sugar maple-basswood; the trees are much lower, usually in open stands, and the undergrowth as a rule includes prairie herbs and shrubs.

A DETAILED MAP

A map of the exact boundaries of the Big Woods was deemed necessary, first for the clues it might suggest as to the causes of such limits themselves, and second, as a record of the original vegetational types, the indications of which are rapidly becoming effaced with the development of agriculture.

In 1873, Winchell and Peckham described the limits of the Big Woods. This account, although brief, is fairly accurate as far as it goes, and seems to be the earliest attempt to delimit this region.

More recently an attempt has been made to map the distribution of the important plant associations of Minnesota by F. J. Marshner, who has used land office records as a source of data. This unpublished map is in the possession of the Lake States Forest Experiment Station, University Farm, St. Paul, Minnesota, and the writer has made use of it to get a general idea of where to expect forest transitions in the Big Woods area.

In a number of cases, there are wide discrepancies between Marshner's map and the writer's (Fig. 3). Apparently some of the land office records are unreliable, or else difficult to interpret. It is a case of evidence based on old records vs. evidence of relic groves existing today. The latter would seem more trustworthy. For example, in a number of cases the writer found

old oak groves in regions indicated on Marshner's map as sugar maple-basswood. One can hardly doubt the reliability of an oak grove as an indicator of an original vegetational type, for oaks are seldom planted by man in this region. If they were, they would undoubtedly be set in rows; and, in any event, had they been planted immediately when the land was first claimed, they would not have had sufficient time to attain large size. Similarly, an irregularly spaced and uneven-aged group of trees belonging to the sugar maple-basswood type would hardly be found today in a region which was oak forest in comparatively recent time, except in the case of fire influence which will be discussed later.

The map was constructed as follows: County maps were used as a base, and almost all the passable roads in the region of the forest's boundaries were traversed. One person operated the car while the other recorded the forest indicators on the maps by means of convenient symbols. For the most part, sufficient indicator groves still exist to make it possible to plot the original distribution with great accuracy, but at times the lack of good indicators made the task of fixing a definite line on the maps quite difficult. The transition between sugar maple-basswood and mixed oak communities is so distinct that little difficulty was encountered in plotting this part of the boundary. The transition between sugar maple-basswood and prairie is equally as clear cut. The bur oak forest merges so gradually with the sugar maple-basswood in some places, however, that the writer has arbitrarily placed the line at a point where bur oak and the sugar maple-basswood species seem approximately equal in density.

No attempt has been made to show sugar maple-basswood areas outside of the Big Woods area. Neither has attention been paid to the occasional patches of bur oak forest which occur within the Big Woods. These, including a strip along the gravelly terraces of the Minnesota River, must owe their existence to local areas of poor soil. This inference is based on the soil studies to be later described.

The field data were transferred from the road maps to a tracing of a U. S. Geological Survey map of Minnesota. The map in final form is seen in Figure 3.

FACTORS LIMITING THE EXTENT OF THE BIG WOODS

CLIMATE

It is generally conceded that certain phases of the moisture factor (influenced in part by temperature), acting upon the water balance of plants, exert the most potent influence in determining the distribution of the larger units of vegetation. For the state of Minnesota, Purcell's official precipitation map (1915) shows a regular decrease in total precipitation from east to west. In the latitude of the Big Woods the range is from 75 cm. at the

eastern edge of the state to less than 60 cm. at the western edge. There is also a definite gradient in seasonal distribution, the percentage occurring during the summer months (April-October) increasing steadily to the west (Kincer, 1922)—an approach toward the type characteristic of the grassland region as a whole.

Another of Kincer's maps exhibits an additional characteristic of the precipitation gradient which is significant—the number of times when periods of drouth (defined as 30 consecutive days with less than 0.25 inches of precipitation in 24 hours) occurred between March 1 and September 30, 1895-1914. At the eastern edge of the state, such drouths occurred 18 times in the 20 years, while at the western edge they happened approximately 27 times.

Thorntwaite's (1931) map of the climates of North America constitute a more recent statement of the westward increase in xericism in this region. In the latitude of the Big Woods the western part of Minnesota is classified as subhumid and microthermal with a deficiency of precipitation at all seasons, while the eastern part is similar but has adequate precipitation at all seasons.

That climate, and especially the moisture factor, is the controlling influence in determining the western limit of the Big Woods is plainly shown by the gradual reduction of stature of the trees from east to west. This became evident during the course of preliminary field trips, and a quantitative study of the feature was accordingly planned. At 39 locations, well scattered over the Big Woods, measurements were made of the forest height. Five or six representative trees in each stand were measured with a U. S. Forest Service standard hypsometer, and the average of these was taken as representing the height of the entire stand. No trees were measured which had not to all appearances matured under closed forest conditions, and care was taken to select stands on well-drained upland, for the trees are invariably taller near streams or lakes.

When these 39 measurements are plotted on a map of the Big Woods (Fig. 4), a definite gradient is evident, the height of the forest diminishing from east to west. The total range is from 51 to 89 feet, the former stand being near the edge of the prairie, and the latter near the eastern edge of the Big Woods. West of an arbitrary line drawn along the longitudinal axis of the Big Woods area, the average height of the forest is 68 feet, while to the east of this line the average is 77 feet.

The fact that the trees at the western edge of the Big Woods are still almost 60 feet in height suggests that, although climate is too adverse to permit optimum development, the forest actually does not reach its climatic limit.

It was felt at the beginning of the study that it would be desirable to obtain precipitation data more directly related to the Big Woods than those available in the Weather Bureau record, and, in particular to measure evap-

oration, for which the Weather Bureau furnishes no data. The author, therefore, established for the measurement of precipitation and evaporation a series of five stations extending in a line from the edge of the prairie on the west to a point in the mixed oak forest east of the Big Woods some 52 miles distant from the first.

The locations of the 5 stations were as follows: I, 3 miles west of Glencoe in McLeod County; II, 2 miles north of Young America in Carver County; III, just south of St. Bonifacius in Carver County; IV, 2 miles east of Deep Haven in Hennepin County; and V, in Minneapolis in Hennepin County (see Fig. 4). All stations were located in open truck gardens to obtain uniformity in the surroundings and to insure against vandalism. Rain gauges of the type described by Cooper (1917) were constructed by soldering a tin funnel into the top of a kerosene can, each funnel having a vertical tin collar soldered to its rim to prevent loss by splashing within the funnel. Approximately 200 cc. of kerosene within the can prevented evaporation of collected rain. The mouths of the funnels were carefully levelled at every reading. At each station two spherical Livingston atmometers were mounted 1.5 m. above the ground and 2 m. apart. Each atmometer was equipped with a rainproof valve, and was standardized before and after use. An additional pair of atmometers was kept in the Minnetonka Woods and read on the same days with the 5 stations. A comparison of the figures in the forest with those of station IV (located 2 miles to the east in the open) gives an approximation of the influence of forest cover on evaporation at 1.5 m. above the ground, and also serves, when compared with similar data from other parts of the deciduous forest, as a comparative measure of the degree of mesism attained by this community.

It was planned to take readings of the instruments at each station, at bi-weekly intervals, during the growing seasons of 1933 and 1934. In 1933 a serious but unavoidable break in the observations occurred, due to illness. The data for that year have consequently been discarded. During the first two weeks of operation in 1934, an unusually severe drouth completely dried up all the atmometers of the transect. For this period (May 19 to June 2) total evaporation was well over 900 cc. at all stations.

TABLE 15. Precipitation-evaporation transect of the Big Woods, June 2 to September 22, 1934.

| Station | Precipitation | Evaporation |
|------------------------|---------------|-------------|
| I | 19.1 c.m. | 5030 cc. |
| II | 22.2 | 4783 |
| III | 24.2 | 4150 |
| IV | 20.6 | 4047 |
| V | 13.0 | 4992 |
| Minnetonka Woods | ... | 2369 |

The precipitation total for the summer of 1934 gives little suggestion of a gradient across the Big Woods. That a gradient exists here in both total precipitation and its seasonal distribution has been indicated by the Weather Bureau (Purssell, 1915; Kincer, 1922). It must therefore be concluded that this precipitation gradient as a whole is too slight to be detected by 4-month observations along a transect only 52 miles long.

Total evaporation for the summer of 1934 shows a definite gradient decreasing eastward across the Big Woods except for the last station in Minneapolis. This irregularity in the general trend of moisture conditions may possibly be correlated with a peculiarity in the distribution of rainfall at this end of the transect. Records of the U. S. Weather Bureau show that Minneapolis normally has somewhat less precipitation than stations a few miles west of the city, and what is even more significant in explaining the 1934 data, the anomaly was especially pronounced during this season.

POST-PLEISTOCENE HISTORY

The factors which have been of most significance in determining the distribution of vegetational types in southern Minnesota have had their origins in prehistoric time. In order to understand the relative significance of these influences, it will therefore be necessary to consider certain aspects of the history of this region since the Pleistocene epoch.

During the final stages of Late Wisconsin glaciation, central Minnesota was vegetated, at least in part (Cooper and Foot, 1932; Voss, 1934), by the boreal conifer forest. Following glaciation, rather soon according to Gleason (1922), later according to Transeau (1935), a period of warm, dry (xerothermic) climate occurred, which brought about considerable vegetational readjustment in this region. The prairie encroached upon the forested area, forcing the boreal conifer forest to retreat northward and northeastward, and the oak element of the deciduous forest increased to a maximum (Voss, 1934). After the peak of the xerothermic period had passed, the changing climate began to approach the more mesic condition of today (Gleason, 1922). Favored by this climatic trend, the deciduous forest advanced westward and northwestward, invading both conifer forest and prairie.

Such was the general sequence of events. For the region treated in this paper some special features may be pointed out. Recent studies have brought out the rather surprising fact that the soils of the Big Woods, now supporting excellent deciduous forest, possess a definite prairie profile. McMiller et al. (1934) have worked this out for the Big Woods portion of Hennepin County, and the writer's survey of the region affords ample confirmation. The evidence thus points toward the conclusion that the xerothermic period continued for sufficient time to permit development here of a typical prairie profile. Later, with the advance of the deciduous forest, the sugar maple-basswood

type took over these fine-textured prairie soils. Occupation by this community has not resulted in any significant modification of the profile. It is true that today, in the immediate vicinity, prairie is confined to the coarsest soils. Under typical grassland climate, however, with no competition from forest species, the grasses could have occupied the best soils without hindrance.

In contrast to the prairie soils of the sugar maple-basswood area, the soils to the east, supporting mixed oak forest, possess a podsol profile. It might be assumed from this fact that these areas remained uninvaded by prairie during the xerothermic period. There is, however, the possibility that they once possessed a prairie profile which, unlike that of the finer soils, has not held its own against the influence of the invading forest.

East of the Mississippi River in Minnesota, general podsolization of fine as well as coarse soils (Cooper, 1935) suggests that the prairie invasion of the xerothermic period did not reach this region.

FIRE

The latest important climatically controlled phase in the post-glacial history of the vegetation has been the westward advance of the deciduous forest at the expense of the prairie. The actual boundary of the forest today, however, is obviously not a climatic one. The forest has, in comparatively recent time, extended farther westward, and could do so today were it not for the inhibiting effects of fire. The bulk of the damage due to this agent came through the conflagrations started by the plains Indians in connection with hunting and warfare.

The climatic limit for forest growth, at present and in past time, is, of course, a matter of conjecture. The gradient in forest height across the Big Woods is, however, suggestive. As previously mentioned, the stature of the trees decreases from nearly 80 feet at the eastern to about 60 feet at the western edge. The abrupt western edge with the trees still 60 feet tall suggests a hypothetical projection of the gradient farther westward. This leads us to infer that 100 miles west of the Big Woods the trees, if present, would be reduced to the height of shrubs. If this reasoning is valid, the present potential climatic limit of the forest is approximately 100 miles west of the present limit. It is possible that the destruction of the forest itself might have steepened the gradient of the top of the portion remaining, in which case the climatic limit would be somewhat more than the 100 miles westward assumed above.

Vegetational evidence of the influence of prairie fires in extending grassland eastward at the expense of the forest is abundant in the transition region as a whole, and follows three lines: (1) rapid natural afforestation with the development of artificial fire barriers such as roads and cultivated fields, (2) forest species persisting as relics in prairie communities, and (3) restriction

of fire-intolerant plants to the leeward of natural fire barriers such as streams, lakes, and marshes.

It has been possible to apply only one of these—the third—in the present study, the first two being unavailable because of intensive cultivation along the western and southern edges of the Big Woods. Examples of protection of vegetation by natural fire-barriers are abundant and unmistakable around the western and southern edges of the forest. A detailed map (Fig. 3) shows close correlation between the limits of the forest and such features as lakes and river valleys. At the northwestern corner the correspondence is not close enough to explain completely the limits of the forest here, but as we go southward the fires have apparently had increasingly greater influence, until in Nicollet County the forest has been almost completely eliminated on the windward side of the Minnesota River.

The behavior of sugar maple, the most fire-sensitive species, at the western edge of the Big Woods is particularly noteworthy. Here it is completely absent in those places where fire barriers are so ineffective that they have served only to lessen the intensity of the burning. In such places a gradual transition occurs from pure sugar maple-basswood forest to bur oak savanna, and it is always the sugar maple which is the first to drop out. Red oak shows a similar behavior, and is probably the second most fire-susceptible tree.

Where fire barriers are very effective, both sugar maple and red oak are mixed with their usual associates in island-like areas well out in the prairie.

The peculiar courses of the Minnesota and Cannon rivers have apparently played a major rôle in determining the southern end of the Big Woods. Fires starting south of the Minnesota River and travelling in a general eastward direction in this latitude met the river at an acute angle which must have had little effect except to shunt them further southward along a strictly controlled course parallel to the river.¹⁶ This deflection probably concentrated the effects of the fires as they met and followed along the river.

At the city of Mankato the Minnesota River makes a sharp turn northward, and, had not another barrier, the Cannon River, been present, the concentrated fires would no doubt from this point have come again under the direct influence of the wind and fanned out over a wedge-shaped path, increasing in width eastward.

The Cannon River is a small stream, but it meanders through a wide marshy valley cut by a glacial river during the Pleistocene. The peculiar course of this excellent fire barrier has apparently limited the lateral northward spread of the fires as far as the vicinity of Northfield. On the north side of the valley, handsome stands of sugar maple-basswood forest extend to the edge of the marsh, while on the bluffs across the valley the vegetation

¹⁶ Grass fires in this region occur chiefly at the beginning and end of the growing season. In April the prevailing winds in southern Minnesota are from the northwest; in August and September they are divided between southwest, south, and southeast (Purssell, 1930).

is prairie with a few patches of bur oak savanna. Fires which approached the Big Woods from the south would likewise be kept entirely out of the area by the barrier formed by the Minnesota and Cannon rivers.

The gradual reduction of mesic forest to prairie through the agency of fire probably proceeded through a definite series of stages. On the east side of the Big Woods, the writer discovered an area which seems to indicate the effects of a short period of burning on the sugar maple-basswood community.

This forest is liberally sprinkled with very large bur oaks (*Q. macrocarpa olivaeformis*), which, judging from their forms, must have developed under savanna conditions. Arising from the uppermost of the large horizontal branches are erect limbs which obviously have developed since other trees, growing up, have converted the savanna into a closed forest. The others are almost entirely *Tilia* and *Ostrya*. A conspicuous and significant feature is that the trunks of these two species usually occur in clusters.

Since this timber is in a region where one would, for climatic and edaphic reasons, expect sugar maple-basswood forest, and from the actual existing conditions as described above, the writer feels that the following interpretation is the only possible one. Repeated burning must have eliminated fire-sensitive species (*Acer*, if present, entirely and *Ulmus americana*, *U. fulva*, and *Quercus borealis maxima* partially), kept in a thicket stage those species (basswood and ironwood) whose roots remained living and produced sucker sprouts after each fire, and permitted bur oak with its thick, fire-resisting bark to develop to unusually large size due to the freedom from competition on such a favorable site. Approximately half a century ago the burning ceased, permitting the stump sprouts of *Tilia* and *Ostrya* to grow rapidly into an even-aged forest which overtopped the massive old bur oaks and caused the production of the peculiar vertical branches previously described.

Severe prairie fires, which have undoubtedly occurred for centuries, have caused still more extreme retrogression in such regions as that south of the Big Woods. Here, the sugar maple-basswood forest has been completely replaced by bur oak or even prairie. The retrogressive stages must have been similar to the following:

1. Elimination of maple from the forest (with the first burning)
2. Elimination of the elms and red oak; reduction of basswood and ironwood to a scrub or sprout thicket
3. Replacement of sprout thicket by bur oak, and entrance of grassland herbs
4. Elimination of bur oak (with severest burning)

Summarizing briefly, the distribution of vegetation at the western and southern edges of the Big Woods indicates that these boundaries have been determined largely by the presence and configuration of fire barriers which have kept prairie fires from destroying the forest to the leeward. But for

the influence of fire, the Big Woods and its fringe of bur oak along the western edge would extend somewhat further westward, and much further southward. Evidences of fire control are less pronounced at the north end of the western boundary. In the explanation of the north and east boundaries other factors must be invoked.

SOIL

Previous mention has been made of the abruptness of the transition between the Big Woods at its eastern and northern edges and the adjacent mixed oak forest. Such a boundary is generally due either to fire, soil, or topography. This particular transition, abrupt as it is, cannot be attributed to fire, since there is no correlation between vegetation and fire barriers and because the less mesic forest lies to the leeward of the more mesic. It is therefore necessary to appeal to the other two factors—soil and topography.

Soil samples were collected from 29 stations in the Big Woods, well distributed along the northern and eastern edges, and from 29 stations just over the transition line within the mixed oak forest (see locations in Fig. 4). In each, two or three cores were collected to a depth of 3 feet. The profiles were arbitrarily subdivided so that the samples represented cores of the 0 to 6 inch, 6 to 12 inch, 12 to 24 inch and 24 to 36 inch horizons.

Approximately one-half liter of soil was collected in a paper bag for each sample. These were air-dried in a chemical-free laboratory and then passed through a 2-millimeter screen to mix the samples thoroughly and to remove skeletal material. A total of 676 samples were collected.

Each sample was tested for phosphate, pH, and moisture equivalent. Determinations of available nutrients other than phosphates would also be very desirable, but satisfactory methods of estimation have not to my knowledge been devised. It is true that a number of tests have been described, but the results of these methods usually are not substantiated by experiments in the field, which is the ultimate and final test of the significance of the method. Rost and Pinckney (1932) have applied Bray's phosphate test (1929) to Minnesota soils, and found that about 70 per cent of all experimental plots averaging "medium," "doubtful," or "low" responded to phosphate fertilizer, while only 27 per cent of those averaging "high" responded.

Available phosphate. Rost and Pinckney's work indicates that in this region at least, the critical point in the series of averages is between "medium" and "high." According to this interpretation, nearly all of the forest soils of this region were found to be well supplied with available phosphates. The differences in phosphate content of the soils on the two sides of the eastern and northern boundaries of the Big Woods is too slight to be of significance in explaining the distribution of the forest communities.

Reaction. The reaction of the samples was tested by the quinhydrone

electrode method. It is now a well established fact that air-drying of soils alters the pH values. Achromeiko (1928) found that the original pH of such dried samples can be restored if the samples are moistened 3 to 7 days before making the determinations. Bailey (1932) has more recently made an extensive study of the means which should be employed to restore the pH values of air-dried soils. His method of submerging the samples 18 to 24 hours in distilled water before testing seemed most applicable to the soils of this region, and was used in the present study. Reaction tests of the soil samples are classified in Table 6.

TABLE 16. Reaction of the forest soils as pH.

| Forest Region | | Depth in Inches | Total Samples | 5.0- 5.5 | 5.5- 6.0 | 6.0- 6.5 | 6.5- 7.0 | 7.0- 7.5 | 7.5- 8.0 | 8.0- 8.5 |
|------------------------|-------------------|--------------------|------------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| Big Woods | | 0-6 | 82 | 2 | 1 | 10 | 34 | 31 | 4 | .. |
| | | 6-12 | 82 | 4 | 16 | 23 | 23 | 16 | .. | .. |
| | | 12-24 | 82 | 10 | 20 | 24 | 14 | 14 | .. | .. |
| | | 24-36 | 81 | 8 | 25 | 20 | 10 | 8 | 9 | 1 |
| Mixed Oak Forest | N. of Minn. R. | 0-6 | 49 | 1 | 7 | 13 | 17 | 10 | 1 | .. |
| | | 6-12 | 49 | .. | 13 | 14 | 15 | 5 | 2 | .. |
| | | 12-24 | 49 | 1 | 9 | 20 | 9 | 6 | 4 | .. |
| | | 24-36 | 49 | 1 | 7 | 24 | 3 | 2 | 8 | 4 |
| | S. of Minn. R. | 0-6 | 28 | 2 | 5 | 9 | 10 | 1 | 1 | .. |
| | | 6-12 | 28 | 1 | 13 | 10 | 2 | 1 | 1 | .. |
| | | 12-24 | 27 | 1 | 14 | 4 | 3 | 1 | 4 | .. |
| | | 24-36 | 28 | 1 | 12 | 2 | 5 | 1 | 5 | 2 |

All of these soils may be characterized as circumneutral in reaction, with a definite leaning toward the acid side. As in the case of the phosphate studies, there is too little difference between the reaction ranges of the forest types to be of significance in determining distribution.

Moisture equivalent. Moisture equivalents for the soils were determined by the Briggs and McLane (1907) method. With each group of samples simultaneously centrifuged, a pair of check samples of known moisture equivalent was included. Whenever the results from the latter varied from their true percentages, the unknowns were again tested until their checks gave the correct values (Table 19).

Along the northern and eastern edges of the Big Woods there is a difference in the water-holding power of the soils of the two forest types in the portion north of the Minnesota River, but south of this point there is very little difference in this respect between sugar maple-basswood and oak forest soils. It will be most convenient to discuss the two parts of the transition line separately.

North of the Minnesota River, most of the oak forest subsoil samples are

TABLE 17. Moisture equivalents of the forest soils. The modal classes of the horizontal arrays are italicized.

| Forest Region | | Depth in Inches | Total Samples | Moisture Equivalent Per Cent Classes | | | | | | | | | |
|------------------------|-------------------------|--------------------|------------------|--------------------------------------|---------|----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| | | | | 0- 4 | 4- 8 | 8- 12 | 12- 16 | 16- 20 | 20- 24 | 24- 28 | 28- 32 | 32- 36 | 36- 40 |
| Big Woods | | 0- 6 | 83 | .. | .. | 1 | 11 | 24 | 22 | 16 | 8 | 1 | .. |
| | | 6-12 | 83 | .. | .. | 8 | 30 | 21 | 17 | 7 | .. | .. | .. |
| | | 12-24 | 83 | .. | .. | 8 | 23 | 17 | 24 | 8 | 3 | .. | .. |
| | | 24-36 | 82 | .. | 5 | 6 | 16 | 14 | 20 | 14 | 6 | 1 | .. |
| | | 0- 6 | 49 | .. | 10 | 8 | 12 | 16 | 2 | .. | 1 | .. | .. |
| Mixed Oak Forest | N. of Minn. River | 6-12 | 49 | 4 | 18 | 8 | 9 | 7 | 3 | .. | .. | .. | .. |
| | | 12-24 | 49 | 11 | 18 | 7 | 5 | 2 | 4 | 2 | .. | .. | .. |
| | | 24-36 | 49 | 18 | 14 | 3 | 7 | 2 | 3 | 2 | .. | .. | .. |
| | S. of Minn. River | 0- 6 | 34 | .. | .. | 2 | 7 | 8 | 9 | 3 | 2 | 2 | 1 |
| | | 6-12 | 34 | .. | .. | 3 | 12 | 7 | 5 | 4 | 3 | .. | .. |
| | | 12-24 | 34 | .. | .. | 5 | 4 | 11 | 8 | 4 | 1 | 1 | .. |
| | | 24-36 | 34 | .. | 1 | 4 | 9 | 4 | 9 | 4 | 1 | .. | 2 |
| | | | | | | | | | | | | | |
| | | | | | | | | | | | | | |

coarser (assuming the moisture equivalent to be an indicator of texture) than any encountered in the Big Woods. Two factors might be offered to explain the relatively few cases where the moisture equivalent ranges of the two regions overlap. Since the soils of this region are derived from several layers of glacial drift varying widely in thickness, original nature, and amount of modification, it is quite natural that local areas of fine-textured drift should occur as island-like masses in the coarser materials, which, because of insufficient lateral or vertical extent would be rendered unfavorable by the excessive drainage incurred by the surrounding coarse soil. Again, the overlapping of texture ranges was favored by the locations of the soil stations, for Big Woods and oak forest soils were both collected very near the transition line (sometimes less than $\frac{1}{2}$ mile apart) where a minimum of difference between the two forest soils would be expected.

All of the Big Woods occurs on thick Young Gray Drift of Late Wisconsin age. North of the Minnesota River the edge of the Big Woods corresponds closely with a rather abrupt thinning of this drift. The mixed oak forest soils have been derived from either older, coarse Red Drift of mid-Wisconsin age, with a thin layer of Gray Drift over the surface, or else outwash material derived from both parent bodies. This correlation between the forest transition and the abrupt thinning of the Young Gray Drift seems causal.

The region where soil texture seems to be important begins on the east side of the Big Woods at the Minnesota River and extends northward around the north end and down the west side to central Meeker County. Beyond this point no samples were taken for two reasons: (1) south of here the lim-

its of the Big Woods begin to show more constant correlation with fire-barriers, and (2) *Quercus ellipsoidalis* extends rather conspicuously around the Big Woods to this point, beyond which bur oak is practically the only species in the narrow strip of forest between the sugar maple-basswood community and prairie. Since the fire-sensitive *Quercus ellipsoidalis* is absent, and the dependence of the Big Woods limits on fire barriers becomes very conspicuous, it was concluded that southward from central Meeker County, the primary factor limiting the Big Woods was fire.

The writer has as yet little to offer in explanation of the transition from sugar maple-basswood to mixed oak forest along the portion of the east boundary between the Minnesota River and Northfield. Analyses of the soils on the two sides of the line are very similar; the position of the oak forest to the leeward of the Big Woods and the abundance of *Quercus ellipsoidalis* preclude the possibility of fire influence.

There is, however, a definite difference in topography. The region to the west of the line is extremely hilly, being a part of the pronounced subterminal moraine of the Young Gray Drift. To the west of this boundary is an undulating till plain of the same kind of drift. The region of the terminal moraine seems to have a low water table, for the depressions between the knobs seldom contain lakes, and in this respect differs strikingly from the lake-dotted till plain. I venture the suggestion that the low water table may have prevented the establishment of the mesic type of forest on the uplands. Ravines in this region are heavily wooded with sugar maple-basswood forest, but this is hardly significant since the same holds for practically all ravines of any size in central Minnesota. Beyond this moraine to the east are entirely different types of parent material (outwash, Kansas drift, or Young Red Drift) all of which are characterized by a narrow zone of mixed oak forest beyond which is fire-induced prairie.

In summarizing these soil studies, there seems to be no relationship between soil reaction or available phosphate content and the distribution of forest types in this region. A part of the eastern, and the northern limits of the Big Woods, corresponds closely to the edge of the unmodified Late Wisconsin drift; the soils beyond this edge have a much lower water-holding capacity as a rule. South of the Minnesota River the Big Woods ends at the edge of a moraine, the soils of which seem favorable to sugar maple-basswood forest, according to the analyses. A low water table or some other condition accompanying the moraine has here inhibited the more mesic forest from the uplands.

DISTRIBUTION OF THE SUGAR MAPLE-BASSWOOD CLIMAX

The northwest portion of the deciduous forest seems to be a complex of closely related communities, with nearly the same list of dominants, and typified by the sugar maple-basswood climax.

On the White Earth Indian Reservation in northern Minnesota, Ewing (1924) has described the climax community of the deciduous forest belt as consisting of *Tilia americana*, *Ulmus americana*, *Acer saccharum*, *Fraxinus pennsylvanica lanceolata*, *Populus tremuloides*, and *P. balsamifera*. The relative importance of the species in the above list is not discussed.

About 22 miles east of this reservation, Lee (1924) has studied the forest successions around Lake Itasca in Clearwater County, Minnesota. He describes a sugar maple-white pine type as one of four virgin communities. This occupies the fertile clay soils, while others are limited to sandy or swampy sites. The important species are *Acer saccharum*, *Pinus strobus*, *Tilia americana*, *Ulmus americana*, *Quercus borealis* or *Q. borealis maxima*, *Q. macrocarpa* (= *Q. macrocarpa olivaeformis*), and *Betula papyrifera*. In this community, white pine owes its existence to local openings in the stand.

Approximately 30 miles east-northeast of Lake Itasca, Kittredge (1934) has described a forest succession on sandy outwash on Star Island in Cass Lake, near the southeast corner of Beltrami County, Minnesota. In this series sugar maple-basswood is climax. The trees, listed in order of importance, are *Acer saccharum*, *Tilia americana*, *Ulmus americana*, *Quercus borealis*, and *Ostrya virginiana*. Basswood has a higher density than sugar maple, but this is attributed to fires in the past. Abundant reproduction of the maple seems to indicate that if undisturbed it becomes most important.

East of the Star Island region, the forest climax of the better soils seems to be a hybrid type of community containing dominants from both the boreal conifer forest and the sugar maple-basswood community. Grant (1934), working in Itasca County, Minnesota, lists the climax species in order of importance as follows: *Abies balsamea*, *Tilia americana*, *Quercus borealis maxima* and *Q. borealis*, *Betula lutea*, *Picea glauca*, *Ostrya virginiana*. He states that this is "probably the climax community over most of the coniferous forest region of Minnesota, except in the extreme northeastern corner of the state." Judging from the studies by Ewing, Lee, and Kittredge mentioned above, the type described by Grant does not extend west of Itasca County. From Itasca County eastward, sugar maple occurs chiefly along lake margins where, according to Rosendahl and Butters (1928) it is protected from unseasonable frosts. The tree reproduces poorly in this northeastern region.

In upper Michigan, the deciduous forest may be divided into several types, one of which is very similar to the Big Woods. Westveld (1933) has studied the composition of these forest communities in the northern peninsula. Here the deciduous forest is found only on loam soils; coarse soils have pines, and

finer ones mixed swamp-conifer and deciduous species. The composition of two stands of sugar maple-basswood in this region, expressed as density percentage of trees 0.5 inch d.b.h and over, is given as follows:

| | On Stambaugh silt loam Per cent | On Iron River silt loam Per cent |
|---------------------------------|---------------------------------------|--|
| <i>Acer saccharum</i> | 75.8 | 63.8 |
| <i>Tilia americana</i> | 10.9 | 10.1 |
| <i>Ostrya virginiana</i> | 4.9 | 3.9 |
| <i>Betula lutea</i> | 0.5 | 7.1 |
| <i>Abies balsamea</i> | 1.6 | 6.2 |
| <i>Tsuga canadensis</i> | 1.4 | 5.4 |
| <i>Ulmus americana</i> | 1.4 | 2.7 |
| <i>Prunus serotina</i> | 3.4 | 0.0 |
| <i>Picea glauca</i> | 0.4 | 0.0 |
| <i>Thuja occidentalis</i> | 0.3 | 0.0 |

McIntire (1931) gives the composition (expressed as basal area in sq. ft. per 1,000 sq. m.) of a stand of sugar maple-basswood on Trenary loam in Alger County, northern Michigan:

| | |
|------------------------------|-------|
| <i>Acer saccharum</i> | 27.63 |
| <i>Tilia americana</i> | 3.34 |
| <i>Ulmus</i> | 2.73 |
| <i>Betula lutea</i> | 1.06 |
| Others | .82 |
| Total | 35.22 |

In lower Michigan, the climax forest of better soils is dominated by *Acer saccharum*, *Fagus grandifolia*, *Tilia americana*, *Tsuga canadensis*, *Betula lutea* and others (Quick, 1923). On the west side of Lake Michigan, *Fagus* is first to drop out of the climax forest (see list of species by Zon and Scholz, 1929), and next *Tsuga* and *Betula*. *Tilia*, increasing in relative importance from New England westward (Frothingham, 1915), becomes second to *Acer* beyond the region where *Tsuga* and *Betula* are important.

Sugar maple-basswood forest also occurs in Illinois. Gleason (1912) considers the "hard maple-basswood type of forest" as "the highest type found in central Illinois."

Aikman has described the climax forest community in Iowa (1930) and along the eastern edge of Nebraska (1926) as a red oak-basswood association. In Nebraska the most important trees, in order of importance, are *Tilia americana*, *Quercus borealis maxima*, and *Ostrya virginiana*, while among the others are *Carya cordiformis*, *Fraxinus pennsylvanica*, *Ulmus americana*, and *U. fulva*.

Generalizing from the published accounts reviewed above and from the present study, it seems that the sugar maple-basswood type is the regional climax of the northwest corner of the deciduous forest, in Minnesota, prob-

ably much of Wisconsin, and central Illinois. Approaching the boreal conifer forest, the sugar maple is reduced to a minor rôle and a transitional climax dominated by balsam fir and basswood is characteristic. Approaching Lake Michigan and the main body of the deciduous forest to the east, basswood becomes reduced in relative importance, and hemlock, yellow birch and beech accompany sugar maple as important dominants. Toward the prairie to the south and west, sugar maple drops out of the community leaving basswood, red oak, and ironwood as the chief dominants of a closely related community.

ACKNOWLEDGMENTS

The writer wishes to express sincere appreciation for the coöperation of those who have contributed to the furtherance of this study: to Dr. W. S. Cooper for suggesting the problem and criticizing the manuscript; to Dr. C. O. Rost for helpful suggestions concerning the soil studies; to those residents of the region who have kindly offered the use of their premises for instrumental and vegetational studies and have given useful suggestions of historical nature; and lastly to my wife who has generously shared much of the routine work in the laboratory and in the field.

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THE AGGREGATION BEHAVIOR OF *STORERIA*
DEKAYI AND OTHER SNAKES, WITH ESPE-
CIAL REFERENCE TO THE SENSE
ORGANS INVOLVED

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THE AGGREGATION BEHAVIOR OF *STORERIA DEKAYI* AND OTHER SNAKES, WITH ESPECIAL REFERENCE TO THE SENSE ORGANS INVOLVED

INTRODUCTION

It is often assumed that snakes show no social behavior except during breeding season and at times of hibernation (Prater, 1933). However, if large numbers of certain species are frightened while in an exposed situation they come together to form compact masses. In the case of the common brown snake, *Storeria dekayi*, the individuals entwine themselves into a large cluster and the entire group can be picked up by taking hold of only a portion of the mass. Other species, such as *Thamnophis butleri*, do not react to the same degree and the resulting masses are consequently not as compact. The tendency to form these masses in exposed situations after frightening is found in both the young and mature individuals regardless of the period of the year.

Aggregation as the result of disturbance probably rarely occurs in nature because there are usually sufficient means for retreat. There is, however, another type of response which doubtlessly occurs frequently in nature and has also been noted under laboratory conditions, namely aggregation when environmental conditions are unsuitable.

Although *Storeria dekayi* and *Thamnophis butleri* are as well known as most North American snakes the tendency of these species to aggregate under the above conditions has not been previously described. The aggregation behavior of animals has recently been critically reviewed (Allee, 1931). Our knowledge of the mechanism of aggregation in vertebrates higher than fishes is very poorly known. Hence it has seemed desirable to analyze the behavior in the snakes available to us in series. The recent works of Baumann (1929), Kahmann (1932) and Wiedemann (1932) have thrown new light on the rôle of the sense organs in the feeding reactions of serpents. In view of these studies it has seemed desirable to make some comparison between the feeding and aggregating behavior of the species utilized in the present study.

THE FORMATION OF AGGREGATIONS IN *STORERIA DEKAYI*

The compact aggregations of *Storeria* as above described may be readily induced in groups of individuals at temperatures between 18° and 26° C. by removing all covering from the floor of the cage and then jostling the cage. The response is also in evidence when certain environmental conditions are altered. If large numbers of *S. dekayi* are left undisturbed in large cages containing sand and moss of various degrees of dampness they will usually

be found in clusters of about 10 to 15 individuals. Most of these clusters are found between the drier and damper layers of moss. If these layers are disturbed the clusters will break up into approximately 4 to 5 individuals in a group. It may be assumed that these aggregations which form in the absence of any disturbance are due to snakes, coming together in regions of optimum conditions of humidity and temperature. Nevertheless, when humidity conditions throughout the mass are equalized or the sand uniformly dampened, the snakes still come together to form clusters. A study of a large series of individuals under a wide range of humidities and temperatures made it clear that *S. dekayi* exhibits a well marked tendency to aggregate with others of its own species and also that this tendency becomes more marked by disturbing or irritating factors.

AGGREGATIONS IN THE FIELD

It has not been previously recognized that *Storeria dekayi* forms well marked aggregations in the field at all times of the year. Records were made of the degree of aggregation in a large series of individuals collected outside the breeding season at Flushing, N. Y. Excluding the gestating females, which do not aggregate, we found the other 497 snakes distributed as follows:

| Isolated 184 | Aggregated 313 | | | | | | | | | | | |
|--------------|-----------------------|-----|----|----|----|----|----|---|----|----|----|----|
| | In groups of. | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| | Number of Snakes. | 112 | 66 | 48 | 35 | 18 | 14 | 8 | .. | .. | .. | 12 |

In other words, no less than 63 per cent of all the snakes observed outside of the hibernating season and excluding the gestating females, are found aggregated and usually in small groups. Most of these snakes were found under pieces of wood, paper or other detritus. We have included in the above figures only those snakes which were in actual contact. If we should consider all snakes under the same object to be aggregated, the total number of aggregated snakes would exceed 79 per cent. Moreover, 74 per cent of the 497 individuals were found in two areas each approximately 30 ft. square. DeKay snakes were collected at other times and other places. The size of the aggregated groups and the spotty distribution were very similar to that studied in detail in these 2 areas. It will be shown below that the clustering under the same object or within the confines of a limited area may also be considered a manifestation of the aggregation drive.

The most extensive aggregations of *S. dekayi* are those of hibernation. In the fall of 1932, Mr. S. C. Yeaton found the first hibernation den on a small knoll on the edge of a swamp on the outskirts of Flushing, N. Y. The den was apparently an old rat burrow which faced south. Although the burrow

was only 11 inches deep no less than 76 *S. dekayi*, 10 immature *T. sirtalis* and 1 immature *Natrix sipedon* were taken from the bottom of the single chamber which ended blindly. So far as we are aware this is the first time a hibernating den of *S. dekayi* has been reported. The fact that this species may hibernate with a species with which it does not ordinarily associate during the greater part of the year is of considerable interest and will be again considered in a later part of the report.

This series of *S. dekayi* taken in hibernation, ranged from 110 to 325 mm. in total length on February 14, 1933. When the total lengths of all the individuals in the series were plotted it was found that there were 2 distinct modes with one mean at 155 mm. and the other at 271 mm. There were 56 snakes in the mode having the smaller mean and 24 in the other. No individuals fell in the range between 210 and 230 mm. When the sexes were plotted separately no well defined difference was noted in the curve. The young of *S. dekayi* have been reported in one case to range from 102 to 110 mm. at birth on August 13 (Force, 1930) and in another case, to range from 100 to 107 mm. shortly after birth on August 17 (Shields, 1929). One *S. dekayi* collected in November 1933 and kept in our laboratory, gave birth to 5 young, 3 of which were still-born, on March 20, 1934. The female was 310 mm. in length with the largest young measuring 80 mm. and the average of the 5 being 78 mm. It is apparent that the individuals in our smaller mode were young of the first year. Since *Storeria* breeds normally in the early spring, the individuals in our smaller mode would obviously not breed the first year of their life. Adult size is apparently obtained, however, by the following fall and hence sexual maturity is presumably reached by the second spring in the life of the species. Direct proof of this contention is afforded by the data presented in Table 1. A snake (103) collected, marked and released in the field October 31, 1933, was 190 mm. in total length. By December 8, 1934, it had grown to 300 mm. in total length. Six other young snakes (Nos. 10, 20, 3, 127, 50 and 119) added over a hundred millimeters to their length between October or November of one year and December of the following year. Only one young snake (No. 80) which lived under natural conditions for over a year failed to add a hundred millimeters to its length.

During the past 2 years of field study over 500 *S. dekayi* were collected and brought into the laboratory and 186 others were marked by cutting off one or more of the subcaudal scales (according to the method of Blanchard and Finster, 1933). These marked snakes were released again so that normal movements and migrations could be further studied. The snakes were found under small pieces of paper, tin, tarpaper and, less often, under stones. They were also found actively crawling around in the grass at different times of the day. The favorable localities were on slopes with southern exposures. In the region where *Storeria* occurred, they were usually observed in groups.

TABLE 1. *Storeria dekayi* found in Den B on December 8, 1934.

| Snake No. | Sex | Size in mm. | Original Location | Date Found | Migration Distance to Den | Size in mm. When Found in Den |
|-----------|-----|-------------|-------------------|------------|---------------------------|-------------------------------|
| 103..... | ♂ | 190 | Region A | 10-31-33 | 60 yds. | 300 |
| 175..... | ♀ | 490 | Region C | 3-22-34 | | 490* |
| 10..... | ♀ | 180 | Region D | 10-26-33 | 450 yds. | 310† |
| 80..... | ♂ | 200 | Region C | 10-30-33 | 1320 yds. | 295 |
| 4..... | ♂ | 315 | Region C | 10-26-33 | 1320 yds. | 315 |
| 20..... | ♀ | 220 | Region B | 10-26-33 | | 326 |
| 3..... | ♂ | 182 | Region C | 10-26-33 | 1320 yds. | 283 |
| 127..... | ♂ | 194 | Region B | 11- 5-33 | | 314 |
| 15..... | ♀ | 315 | Region B | 10-26-33 | | 315 |
| 50..... | ♂ | 177 | Region B | 10-27-33 | | 323 |
| 119..... | ♀ | 208 | Region B | 11- 3-33 | | 346 |

*Found in C, but placed in B, 3-22-34. Therefore no migration.

†D region is located west of B region between B and C.

For example, on one southern slope (Fig. 1) only 2 areas, each approximately 10 feet square, were ever inhabited. One of these areas is in the immediate foreground in Figure 1, while the other is 50 yards west in the background of the above figure. The intervening territory between these 2 areas never yielded any snakes. These 2 regions will be designated as regions A and B in the following discussion. The slope was examined at 2 to 3 day intervals for a period of 3 months. Some of the snakes were brought back to the laboratory for further study; the marked individuals were released where they were originally found or in some instances they were released some distance away. The marked snakes usually remained in the region where they were released providing they were originally found there. However, if they were released in a locality some distance from where they were found, they often returned to the original location. That is, of the 32 snakes marked and released in a foreign territory, 13 of them returned to the original spot over a 70-day period. In other words, about 40 per cent of this group returned to their original locality. The average distance this group moved in a period of 3 days was between 10 and 15 feet. However, our records show that out of the group of 32 snakes, 8 had each migrated nearly 1,320 yards in the period of one week. The return of the above 40 per cent to their original locality leads to the question of whether the movement was a true homing, or was due to a random movement and the accidental termination at the original point where conditions might have been especially favorable.

Occasional observations continued until November 18, 1933, when no snakes were found in any of the favorable regions. The air temperature at this time was 7° C. Since no snakes were to be found on the surface of the ground at this time, region B, an area 10 x 15 feet, where *S. dekayi* had always been found in large numbers, was examined for rat burrows. No



FIG. 1. The habitat of *Storeria dekayi*. Two areas, each approximately 10 feet square were the only sections of this southern slope which were inhabited by the species. One area is in the immediate foreground while the other is 50 yards west, in the background of the picture.

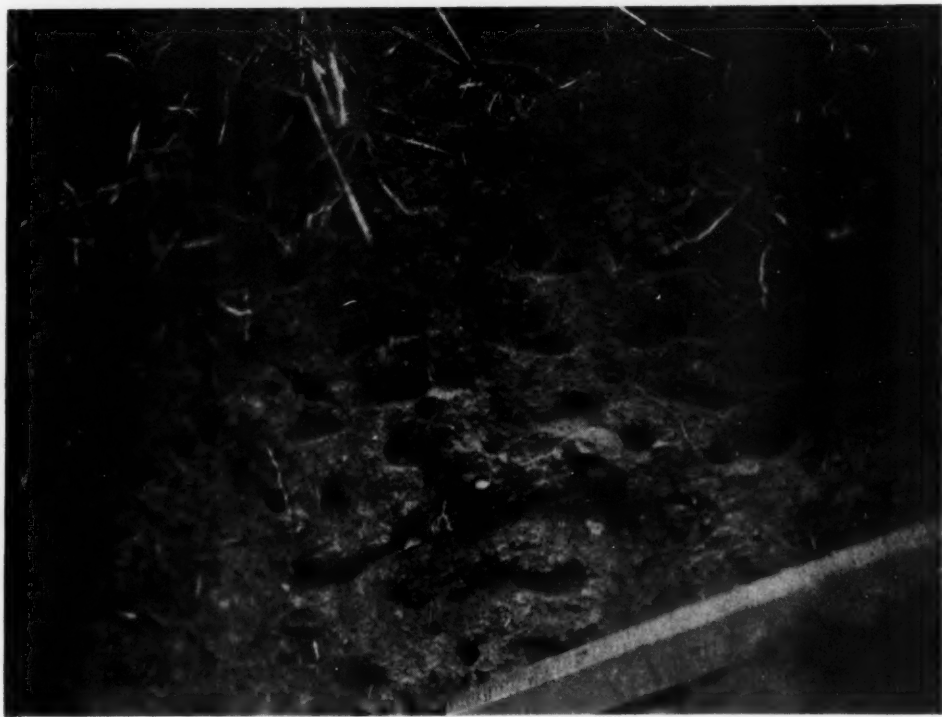


FIG. 2. A part of a hibernating den where *S. dekayi* were found. The ground is undermined, as shown, with ant tunnels in which the snakes were found.

snakes were found in any of the burrows in this or the surrounding area. An excavation was made approximately 3 feet square and 3 feet deep. In this excavation, in small underground channels apparently made by ants, 62 DeKay snakes were found in clusters of 2 or 3 and in a few cases as many as 6. The ground throughout this area was found to be undermined with these tunnels which were approximately 0.5 inch in diameter (Fig. 2). *Storeria* were found in this excavation from a depth of 6 inches to 2.5 feet from the surface. The ground was very dry at the latter depth and at a depth of 3 feet the channels or tunnels were inhabited with black ants (*Formica subsericea*).

On March 20, 1934, the first *S. dekayi* were found since the previous fall. These snakes were again found in the exact region where a large number of snakes had been collected the previous year. This region is designated region C and was located approximately 1,320 yards west of region B. A small rock was found in region C and underneath it a hole, 0.5 inch in diameter, was found which led down vertically to a depth of 2 feet and branched horizontally in two opposite directions. At this depth the sandy soil was mixed with small pieces of rock and tin and had no doubt been filled in some years previous. In these channels and crevices, 45 *S. dekayi* were found in groups of 2 or 3 up to 10 in a cluster. Between the groups of *Storeria* there were several groups of *T. sirtalis*. The snakes were grouped irrespective of sex. Fifteen *T. sirtalis* were removed and in no case were any of them in contact with the *S. dekayi*. Of the 45 DeKays only 10 were snakes which had been marked and released the previous year. These 10 snakes had been released within a radius of 45 feet from the hibernating den. All new *S. dekayi* found in this den were marked and released in regions A and B for further study during the summer.

Up to this time (March, 1934) 186 *S. dekayi* had been marked and released. The regions where all of these individuals had been placed as well as the surrounding territory were carefully examined at intervals of 2 or 3 times per month for the period from April to December. During the months of April to October only 5 of the marked snakes were found again and the distance they had migrated since being marked varied from 12 to 1,320 feet. It is of interest to note that these snakes were at a distance from the regions they had inhabited during the spring or the previous fall. Six marked individuals found during the months of October and November had returned to their original place of hibernation. From these observations it may be concluded that during the summer and early fall months DeKay snakes move about at random. During the months of October and November there is a migration toward the hibernation regions. The region or den selected may or may not be the same one utilized the previous year.

On December 10, 1934, the hibernating den in region A was again exca-

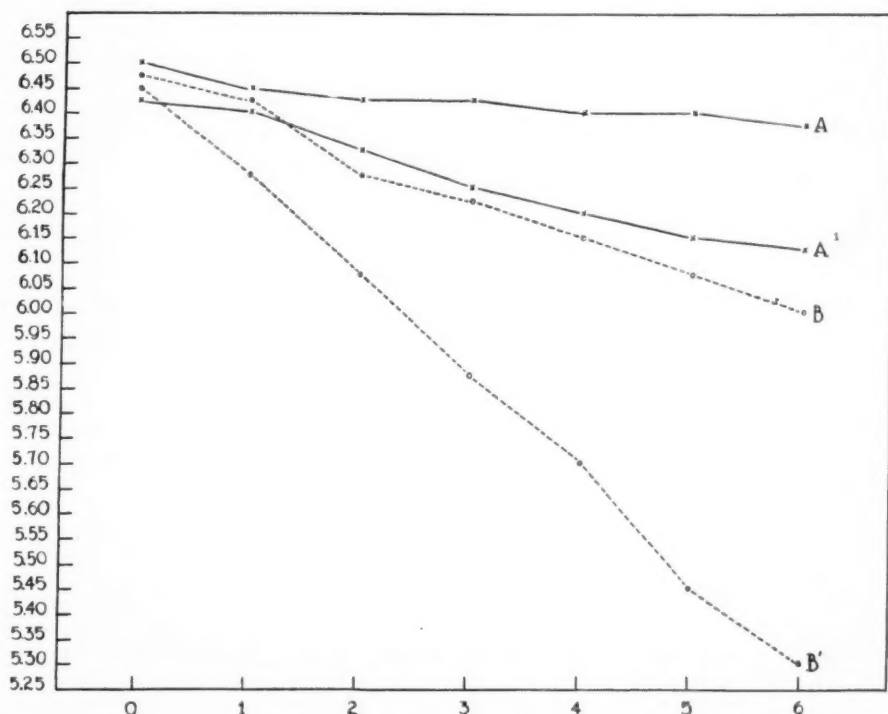


FIG. 3. The average loss in weight of five *S. dekayi* in both the isolated and aggregated condition over a period of 6 hours at constant temperatures. Abscissas, hourly periods; ordinates, average weight in grams; continuous lines A and A', decrease in weight of aggregated snakes at 30 and 35° C. respectively; broken lines B and B', isolated snakes at 30 and 35° C. respectively.

vated. Ninety-seven *S. dekayi* were found in the ant tunnels as previously described. Of this group only 11 were individuals that had been marked. Five were found here originally and released here within 10 to 15 feet from the den. The other 6 individuals had been found elsewhere and placed here (Table 1). From this table it would seem that snakes 20, 127, 15, 50 and 119, having been found in the original location after being released more than a year previous, had returned to their original hibernating den. Since they were not found in this location during the intervening time they had presumably moved away and then returned. But these snakes were all released in 1933 and they were not found in this den area when it was excavated November 18, 1933. It is possible they were overlooked in some channel not completely excavated but it is more probable that they hibernated elsewhere the first winter. From these data it may be concluded that snakes do not necessarily return to the same den year after year. DeKay snakes migrate to a region most suitable for hibernation and this region may or may not be the same den utilized in previous years. This is well shown by the movements of snake No. 175 (Table 1), an individual removed from a den in region C in March and placed in region B at that time. The snake was

found hibernating in region B the following year. No evidence of an attempt to return to region C was disclosed. The remaining snakes as recorded, showed evidence of migration toward the den in region B even though they were originally found in other regions. The latter regions were near other hibernating dens to which these snakes might have returned.

During the months of June and July no aggregates were found in the hibernating or surrounding areas. The adult male snakes and half grown individuals were always found in the open and actively crawling around while the adult females were always found isolated under stones or paper where the ground and dead grass were moist. These females go into seclusion during the last part of the gestating period and remain in one locality until parturition. Six gravid females were found during the last week in June and were observed to remain in exactly the same spot till the last week in July when the young were born. In no case was there evidence that the female had left the rock or paper at any time during this period, since observations were made frequently and notes made of their position under the rocks or paper.

From our field observations on *S. dekayi* it may be concluded that aggregation occurs at all times of the year except, in the case of adult females, during the months of June and July. At this time such females are gestating and isolated from the males or other females. The aggregations found in the ant tunnels or other subterranean channels of the den areas in mid-winter are of course more concentrated than the scattered aggregations of mid-summer, but the mechanism which produces both types of grouping is, we believe, essentially the same. In order to elucidate the various sensory components involved in these aggregations we have performed a series of experiments which will be described below.

LABORATORY CARE OF *Storeria*

A total of 400 *S. dekayi* was collected from these various regions during the past year and brought to the laboratory. They were placed in wood frame cages measuring 21 x 15 x 14 cm. and having glass sides and a screened top. On the tin bottom of the cage 2 cm. of gravel were spread out and 2 or 3 thicknesses of moss were then placed over the gravel. One layer of the moss was always kept moist. A dish of water and a supply of larvae of the meal beetle (*Tenebrio molitor*) and of the wax moth (*Galleria mellonella*) were always kept in the cages. Earthworms were placed in the damp layer of moss from time to time. The water in the cages was changed daily.

A series of *T. butleri* employed for comparison in these studies was composed entirely of adult snakes collected from the vicinity of Olean, N. Y. The smaller series of *T. sirtalis* and *T. sauritus* were taken from several local-

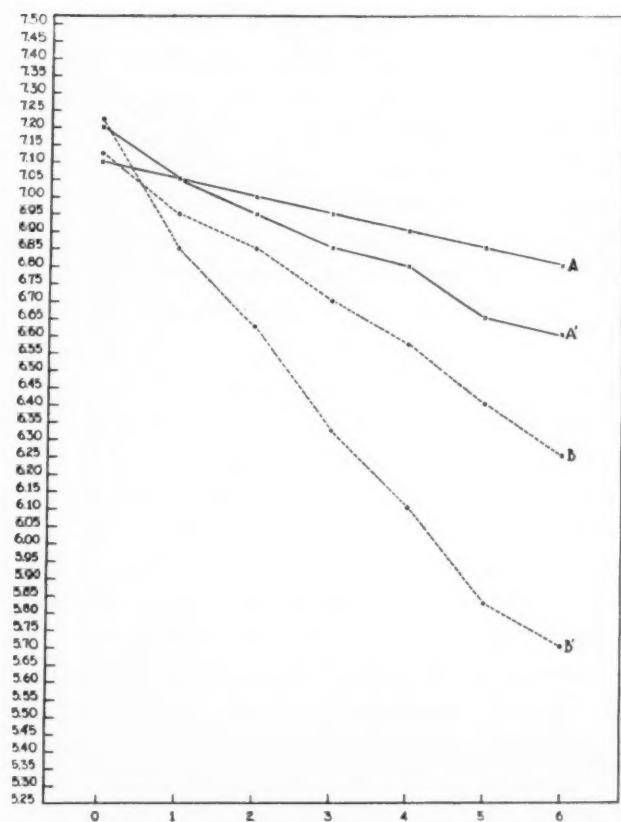


FIG. 4. The average loss in weight of five *T. butleri* in both the isolated and aggregated condition over a period of 6 hours at constant temperatures. Abscissas, hourly periods; ordinates, average weight in grams; continuous lines A and A', decrease in weight of the aggregated snakes at 30 and 35° C. respectively; broken lines B and B', isolated snakes at 30 and 35° C. respectively.

ities in New York State and covered a wide range of age groups. Throughout the work we have noticed no consistent differences in the aggregation response between the sexes or between the different age groups.

RATE OF EVAPORATION DURING ISOLATION AND AGGREGATION

If external environmental factors are primarily responsible for aggregation then the physiological state of the snake must in some way be affected by these changes. A series of experiments was carried out to test several physiological factors which are involved in this grouping response. In this series a comparison between isolated and aggregated *S. dekayi* and *T. butleri* was made over a 6-hour period at temperatures of 30 and 35° C. and relative humidity at 25 per cent, to note the amount of water loss in both species in both the aggregated and isolated condition. The changes in body weight were

used as a criterion in determining the loss of water. An isolated snake was placed in one box while a group of snakes was placed in another box. The boxes in both cases were of equal size, being made of wood and measuring 14 x 11 x 6 cm. and fitted with a sliding cover. The boxes were weighed before and after placing the snake or snakes into them. After recording the above weights the boxes containing both the isolated and the grouped snakes were placed in a constant temperature chamber. The snakes that were used as experimentals had not been fed for 1 week previous to the experiment so as to eliminate as nearly as possible any weight loss due to excretion. The isolated animals used in the tests were also employed as individuals of an aggregate so as to eliminate individual differences. At intervals of one hour each, up to and including the sixth hour after placing the snakes in the constant temperature chamber, the boxes were removed and weighed again both with and without the snakes in them and the snakes were also weighed again by placing them in small paper boxes on an analytical balance. This method of weighing therefore checked the weights of the snakes as well as the containers each successive hour during the experiment. Figure 3 records the average weight in grams of 5 *S. dekayi* over a 6-hour period at temperatures of 30 and 35° C. in both the isolated and aggregated condition. The average loss in body weight in the isolated condition during the 6-hour period was 7 and 17 per cent respectively at temperatures of 30 and 35° C. The aggregated snakes showed a loss of 1.5 and 4.5 per cent per individual over the same period at respective temperatures of 30 and 35° C. Figure 4 records a comparative series of experiments similar to the above but carried out with *T. butleri*. With this species the loss in weight for isolated individuals was 10 to 20 per cent at respective temperatures of 30 and 35° C. and for the aggregated cases 4.2 and 8.3 per cent respectively at the above temperatures. Hence, under similar conditions of temperature and humidity, *S. dekayi* becomes desiccated less rapidly than does *T. butleri*, whether isolated or aggregated.

The results of these tests show that aggregation is beneficial in that it conserves water. As the temperature increases, the result of this grouping phenomenon becomes more and more beneficial. There is a marked difference between the water loss of various species. Since *S. dekayi* is a smaller species than *T. butleri*, a group of individuals of the first species having the same weight as a group of the second should lose more water if the permeability of the skin to water were the same in both forms. The fact that such a group of *S. dekayi* loses less water may be considered an adaptation to the drier habitats occupied by this species. The case is similar to that in lizards where the species living in dry habitats have been found to lose less water through their skin than those frequenting more moist situations (Noble and Mason, 1933).

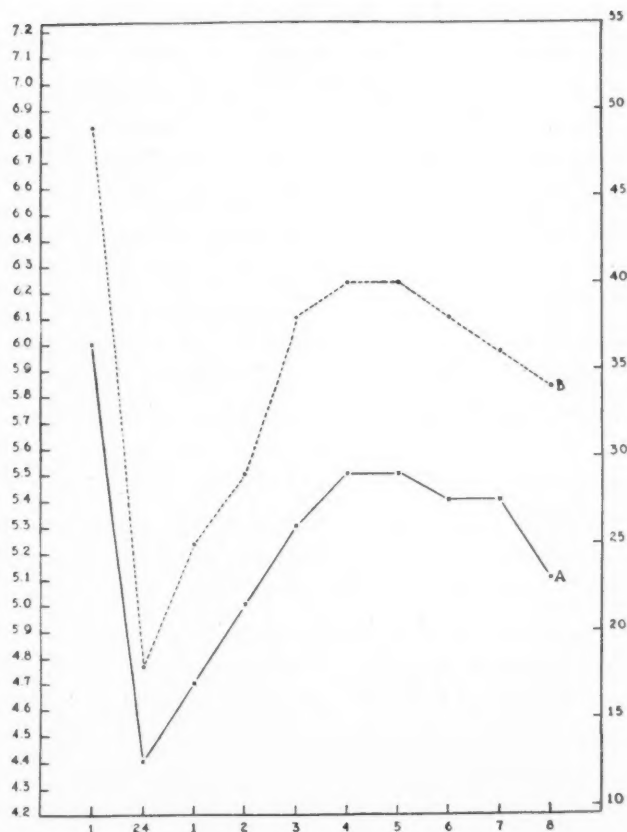


FIG. 5. Correlation between respiration rate and weight loss over a period of 32 hours at a temperature of 30° C. for five isolated *S. dekayi*. Abscissas, 1-24, hours in a dry container and remaining 8 hours in a moist container. Ordinates: left, weight in grams; right, respiratory rate. The continuous line A, weight; broken line B, respiratory rate.

EFFECT OF AGGREGATION ON RESPIRATION

Since aggregation so obviously reduces water loss it presumably influences other metabolic activities such as respiration. The effect of aggregation on the rate of respiration was determined by observing the thoracic or abdominal movement in a group of *S. dekayi* in both the isolated and aggregated condition over a 6-hour period. The snakes, either isolated or in groups of five, were placed in small wood boxes of the same size as used in determining the water content in the previous experiment. These boxes were then placed in a constant humidity and temperature chamber. Throughout the experiment the temperature was kept at 25° C. and the relative humidity at 40 per cent. Table 2 records the average changes in rate of respiration of the same 5 isolated and 5 aggregated *S. dekayi* over a 6-hour period.

It is shown in the table that soon after *S. dekayi* aggregate their rate of

respiration is decreased. With time the decrease continues, but in both isolated and aggregated snakes if the aggregates and the isolated individuals are compared after a 6-hour period the snakes in the aggregate are respiring more rapidly than the isolated ones. Both the isolated and the aggregated groups have come to have lower rates than at the beginning of the experiment, but the decrease is much greater in the isolated series. The decrease in the isolated series is correlated with the greater loss of water. In an earlier series of experiments it was shown that aggregations lose water less rapidly than isolated individuals and in connection with the above studies a series of tests was made to show that aggregations also take up water less readily than do isolated snakes when placed in a moist environment. This series also shows that the respiratory rate is in direct correlation with the water content of the body.

The methods for determining the water intake in the isolated and grouped *S. dekayi* were essentially the same as those used for the water loss determinations except that a lining of moist blotting paper was introduced into the small boxes. The snakes were placed in the small wood boxes, the isolated in one and the aggregate of 3 snakes in the other box. These boxes were placed in the constant temperature chamber at 30° C. and left for 24 hours, at which time they were removed and the respiratory rate and weight of each snake were recorded and compared with the original record. The blotting paper lining the boxes was moistened with 5 cc. of water. The weight of the box was then recorded and the isolated and aggregated snakes placed in their respective boxes which were then replaced in the constant temperature chamber. At intervals of one hour thereafter, the aggregate of 3 snakes as well as the isolated snake was removed, the respiratory rates and weights of each individual recorded and the animals again replaced in the boxes in the temperature chamber. Hourly records were made for a period of 8 hours to correlate the relationship between water intake and respiration. This series of experiments was repeated 5 times with different snakes in the aggregated and isolated conditions and also with the same individuals in the same situations. Figures 5 and 6 record the averages for the isolated and aggregated individuals respectively. These graphs show the loss of weight is correlated with a decrease in respiration. Desiccation tends to reduce both the weight and the respiratory rate. A direct correlation also exists between the increase in weight and the increase in respiration in both the isolated and aggregated series.

It will be noted that the respiratory rate of the isolated snakes is at first very much higher than that of the aggregated individuals but it drops below that of the latter during the 24-hour period. As stated above, the initial high rate is apparently due to the excitement and activity of the isolated individuals. If the isolated snakes are kept moist their respiratory rate will not drop be-

TABLE 2. Comparative respiratory rates of aggregated and isolated *Storeria*.

| Case | Size (mm.) | Resp. | Count (3 tests) | | Average Count | Grouped or Isolated Time | |
|--------|---------------|-------|-----------------|----|------------------|-----------------------------|---------|
| | | 1 | 2 | 3 | | | |
| 1..... | 255 | 60 | 65 | 60 | 61.7 | Isolated | 1 hour |
| | | 60 | 58 | 62 | 60.0 | " | 2 hours |
| | | 40 | 35 | 42 | 39.0 | " | 4 " |
| | | 20 | 18 | 25 | 21.0 | " | 5 " |
| | | 10 | 12 | 10 | 10.6 | " | 6 " |
| 2..... | 305 | 57 | 60 | 55 | 57.3 | Isolated | 1 hour |
| | | 64 | 60 | 62 | 62.0 | " | 2 hours |
| | | 43 | 41 | 38 | 40.6 | " | 3 " |
| | | 30 | 35 | 33 | 32.6 | " | 4 " |
| | | 25 | 30 | 23 | 26.0 | " | 5 " |
| 3..... | 290 | 15 | 12 | 15 | 14.0 | " | 6 " |
| | | 50 | 56 | 54 | 53.3 | Isolated | 1 hour |
| | | 40 | 47 | 44 | 43.6 | " | 2 hours |
| | | 40 | 45 | 40 | 41.6 | " | 3 " |
| | | 25 | 18 | 23 | 22.0 | " | 5 " |
| 4..... | 250 | 20 | 20 | 15 | 18.3 | " | 6 " |
| | | 55 | 58 | 50 | 54.3 | Isolated | 1 hour |
| | | 50 | 48 | 51 | 53.0 | " | 2 hours |
| | | 40 | 45 | 42 | 42.3 | " | 3 " |
| | | 20 | 26 | 23 | 23.0 | " | 5 " |
| 5..... | 205 | 18 | 20 | 20 | 19.3 | " | 6 " |
| | | 28 | 35 | 30 | 31.0 | Grouped | 1 hour |
| | | 30 | 32 | 30 | 30.6 | " | 2 hours |
| | | 26 | 28 | 28 | 27.3 | " | 4 " |
| | | 27 | 25 | 26 | 26.0 | " | 5 " |
| 6..... | 255 | 25 | 25 | 26 | 25.3 | " | 6 " |
| | | 34 | 35 | 35 | 34.6 | Grouped | 1 hour |
| | | 30 | 30 | 30 | 30.0 | " | 2 hours |
| | | 25 | 26 | 25 | 25.3 | " | 4 " |
| | | 25 | 25 | 25 | 25.0 | " | 5 " |
| 7..... | 250 | 24 | 25 | 25 | 24.6 | " | 6 " |
| | | 30 | 32 | 31 | 31.0 | Grouped | 1 hour |
| | | 33 | 32 | 33 | 32.6 | " | 2 hours |
| | | 25 | 25 | 25 | 25.0 | " | 3 " |
| | | 23 | 24 | 23 | 23.3 | " | 5 " |
| 8..... | 290 | 18 | 20 | 20 | 19.3 | " | 6 " |
| | | 36 | 35 | 36 | 35.6 | Grouped | 1 hour |
| | | 33 | 33 | 30 | 32.0 | " | 2 hours |
| | | 30 | 31 | 30 | 30.3 | " | 3 " |
| | | 25 | 26 | 25 | 25.6 | " | 5 " |
| | | 23 | 21 | 25 | 23.0 | " | 6 " |

low that of the aggregated snakes. This is well shown in a series of tests during which 5 *S. dekayi* were placed singly in the standard boxes lined with moist blotting paper. An aggregate of 5 snakes was placed in a similar box without the moist paper. The temperature was held constant and the respiratory rates recorded over a 9-hour period. As shown in Figure 7, the respiratory rate of the moist isolated snakes does not drop below that of the

aggregated. Hence the great drop in the respiratory rate of the isolated snakes on a dry substratum is to be attributed to water loss. More quantitative results concerning the significance of aggregation on respiration in *S. dekayi* have confirmed the above results (Clausen, 1934).

EFFECT OF HUMIDITY ON AGGREGATION

Earlier in this series of studies it was noticed that when the gravel floor of the cages was wet, *S. dekayi* would not burrow. If the gravel was allowed to become very dry they would often be found entirely concealed in the gravel. It was apparent that humidity had an influence on the slow aggregation response which occurs in the absence of any disturbance factor. In order to secure more detailed information on the effect of humidity on this type of aggregation, we have tested a series of snakes in a tank equipped with an apparatus for controlling humidity.

An aquarium having the dimensions 36 x 40 x 60 cm. was provided with a close fitting glass top and sealed with stopcock grease. The aquarium had a bottom of Alberene stone and ends made of the same material. The sides and the top of the tank were of heavy glass. The glass top was held in place with tape. The tank was divided into 2 compartments of equal size by a glass partition which was raised 5 cm. from the gravel which covered the stone floor and thus allowed the snakes to move freely from one compartment to the other. A constant difference in humidity was maintained in the two compartments by pumping dry air into one and moist air into the other. Air was drawn out of each compartment from outlets at both ends of the aquarium by means of an electric pump. After bubbling this air through several vessels of water on one hand and passing it through one or two flasks of calcium chloride on the other, the air was returned to the two compartments of the tank. The apertures for the air intake into the two compartments were made through the glass cover. Glass and rubber tubing carried the air into two large glass tubes which were 15 cm. in length and 4.5 cm. in diameter. One tube was laid on the gravel in the center of each chamber. These tubes will

TABLE 3. The aggregation response of *Storeria dekayi* in relation to humidity.

| Number of Snakes | Temperature in degrees C. | Per Cent Relative Humidity | | Reaction | |
|------------------|---------------------------|----------------------------|----------|----------|----------|
| | | Wet Tube | Dry Tube | Wet Tube | Dry Tube |
| 10..... | 25 | 20 | 20 | 4 | 5 |
| 10..... | 24 | 80 | 65 | 5 | 5 |
| 10..... | 24 | 80 | 75 | 4 | 5 |
| 10..... | 25 | 40 | 40 | 5 | 4 |
| 10..... | 24 | 40 | 20 | 6 | 4 |
| 12..... | 24 | 35 | 25 | 5 | 5 |
| 14..... | 25 | 67 | 43 | 1 | 9 |
| 10..... | 24 | 40 | 32 | 4 | 6 |
| 10..... | 24 | 70 | 28 | 0 | 8 |

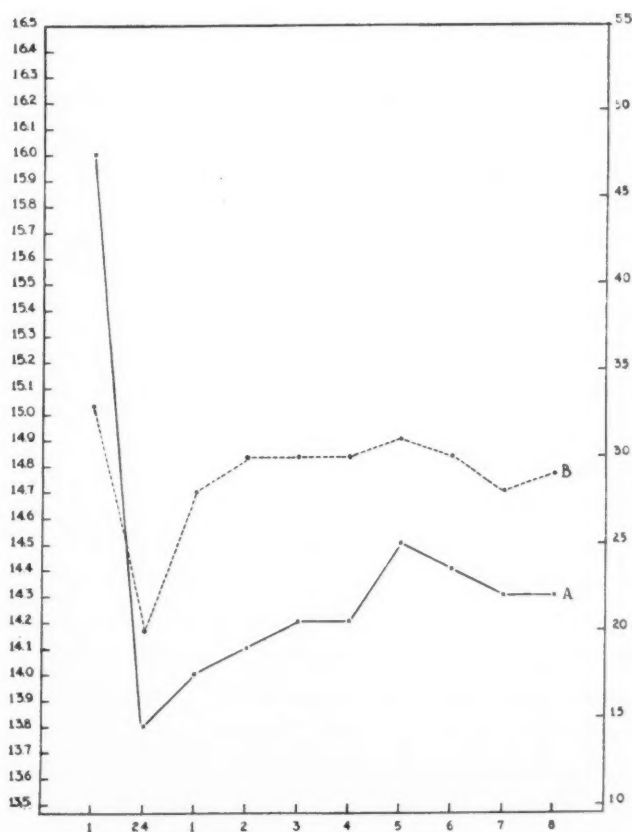


FIG. 6. Correlation between the respiratory rate and weight loss over a period of 32 hours at a temperature of 30° C. for aggregated *S. dekayi*. Abscissas, 1-24, hours in a dry container; 1-8 following, hours in moist container. Ordinates: left, weight in grams; right, respiratory rate. The continuous line A, weight; broken line B, respiratory rate.

be designated as either wet or dry tubes in the following records, depending on which receives the dry or moist air. A thermometer and hygrometer were placed in each compartment. These instruments were tested at frequent intervals throughout the experiment to make sure of their reliability.

In order to secure information on the sensory modalities employed in detecting moisture, a series of snakes with one or more sensory functions eliminated was also tested in this apparatus. In order to eliminate vision, the eyes, in some of the tests, were covered with adhesive tape which was usually blackened with India ink. In some tests a solution of 14 per cent collodion was darkened with ink and painted over the eyes. In a few tests a combination of both methods of blindfolding was utilized. The snakes frequently attempted to remove the blindfolds by rubbing, but after 24 hours they had usually given up these attempts. Tests were made only after 24

hours and only with snakes which showed no evidence of irritation from the blindfold.

The olfactory sense was eliminated by filling the nostrils with cotton plugs smeared with vaseline and then covered with collodion caps. In other tests the tongue, which has recently been shown to aid the functioning of Jacobson's organ, was severed just caudal to its bifurcation. These snakes were not utilized until they had apparently completely recovered from the operation.

In the following tables the results, as obtained with snakes having their sensory organs incapacitated, will be recorded as follows: B, blindfolded; N, nose-stopped; T, tongueless. Where more than one sense organ is eliminated, combinations of the above symbols will be used, i.e., BNT, blindfolded, nose-stopped and tongueless.

The reactions, as obtained under different humid conditions, for normal *S. dekayi* are recorded in Table 3. This table represents only the typical results obtained in a series of 21 tests. The number of snakes aggregating in or near the mouth of each tube is recorded in the table. If the snakes were in the mid-region of the tank no record was made of them. All individual records were made after the relative humidity had reached and maintained a designated point for 5 minutes. The results (Table 3) show that changes in moisture content of the chamber materially affect the aggregation response of snakes. It will be noted that in no case is the total number of snakes in each experiment accounted for at either the wet or dry tube. The reactions were recorded at the end of a 5-minute interval and if the time were extended the entire group would aggregate. When both tubes were of the same or nearly similar humid conditions the number of individuals around each tube was approximately the same irrespective of whether the humidity was extremely high or low. This condition is illustrated in the first 3 series of experiments in the table. When the relative humidity reached 20 per cent or lower the snakes showed a tendency to collect in the more moist region. They were usually active and irritable in this dry atmosphere and moved around continuously as though in search of a more moist region. When the relative humidity reached approximately 40 to 50 per cent the activity and irritation was again evidenced. In this case the snake seemed to be seeking a drier region. From the results of this series of tests, a part of which is illustrated in Table 3, it was concluded that in normal *S. dekayi* the typical grouping response occurs only when the relative humidity lies between 20 and 45 per cent.

For the series of *S. dekayi* with one or more of their sense organs eliminated, the experiments carried out exactly the same as in the normal series, showed that the same maximum and minimum humidity variations

produced similar results irrespective of the sense organs involved (Table 4). It may be concluded therefore, that the response to varying degrees of humidity was not in any way influenced by the sense organs which, as will be shown below, mediate the aggregation response.

TABLE 4. The effect of relative humidity on the aggregation of *Storeria dekayi* deprived of various sense organs.

| *Series | Number of Snakes | Temperature in Centigrade | Percentage Rel. Humidity | | Reaction | |
|----------|------------------|---------------------------|--------------------------|----------|----------|----------|
| | | | Wet Tube | Dry Tube | Wet Tube | Dry Tube |
| B..... | 10 | 25 | 75 | 40 | 2 | 5 |
| | 10 | 25 | 80 | 40 | 2 | 6 |
| | 8 | 24 | 45 | 35 | 4 | 4 |
| | 8 | 24 | 30 | 20 | 6 | 2 |
| N..... | 10 | 24 | 80 | 48 | 2 | 6 |
| | 10 | 25 | 40 | 35 | 4 | 5 |
| | 10 | 24 | 30 | 20 | 4 | 1 |
| T..... | 10 | 24 | 20 | 20 | 3 | 3 |
| | 10 | 24 | 35 | 21 | 6 | 1 |
| | 10 | 24 | 77 | 42 | 0 | 9 |
| | 10 | 25 | 76 | 68 | 4 | 4 |
| BNT..... | 10 | 24 | 32 | 20 | 6 | 1 |
| | 10 | 24 | 79 | 45 | 1 | 9 |
| | 10 | 24 | 64 | 40 | 2 | 8 |
| | 10 | 24 | 45 | 38 | 5 | 5 |

*Type of experimental animal used:

B - blindfolded. N - nose-stopped. T - tongueless. BNT - blindfolded, nose-stopped and tongueless.

The same series of humidity experiments was carried out with *T. butleri*. The sensory functions were again eliminated in some cases and controls were employed as before. Again the eyes, nose, tongue or Jacobson's organs were found not to be indispensable. The range of adaptability to moisture, however, tended toward a higher percentage of relative humidity than in *S. dekayi*. In this species the response occurred between 30 per cent relative humidity as a minimum and 90 per cent as a maximum. These results therefore show that in respect to humidity, *T. butleri* not only have a higher range, but further, a more extensive range as compared to *S. dekayi*.

When snakes of either of the above species are first placed in the tanks and disturbed, the immediate tendency is toward a clustering irrespective of humidity. However, at almost the same time there is a change in the aggregate toward a more desirable region in respect to moisture. The tendency to aggregate on disturbance is apparently initiated and carried out without respect to moisture, but this response is only temporary and is dominated by a response to aggregate in regions of optimum conditions of humidity shortly thereafter.

TEMPERATURE AND AGGREGATION

In an early series of preliminary experiments it was noticed that by casting a strong light (400 watts) from a microscope lamp on the floor of a cage of *S. dekayi*, the snakes would not move into this area. The area illuminated in this case would have a temperature of 65° C. in the center. The above test was carried out at room temperature of 18 to 20° C. However, when the cage of *S. dekayi* was placed in a cooler room, 10° C., the animals would orient themselves around the illuminated area of the microscope lamp, the temperature of the illuminated area still being 65° C. The temperature of the illuminated area was then reduced to 20° C. by passing the light through a water chamber heat filter. When the temperature was reduced to 20° C. these snakes did not move toward the illuminated area. The light factor was then entirely eliminated and the temperature of the previously illuminated area increased to 60° C. In this case the snakes would again orient themselves around the heated area. It seems obvious from these tests that in *S. dekayi* light is not the primary factor but that the temperature also regulates the orientation.

The same experiment was repeated with *T. butleri*. When an area of the cage was illuminated at room temperatures of 18 to 20° C., these snakes would orient themselves around the illuminated area which again registered 65° C. at its center but graded into a wide area of lower temperature along the periphery. These snakes grouped nearer the hot center of the illuminated area than did *S. dekayi*. This was repeated under room temperatures of 10° C. and the same result as above was recorded. The heat factor was again eliminated as in the *S. dekayi* series and *T. butleri* oriented themselves in or as near as possible to the center of illumination. When the heat factor was introduced in the absence of light the orientation pattern was exactly the same as when both heat and light were employed.

From these experiments it is clear that *S. dekayi* will avoid a center of strong illumination while *T. butleri* will move across such areas. This difference in behavior is correlated with the habits of the two species, *S. dekayi* being the more nocturnal in habits.

It was found in the above experiments that temperature was of importance in directing the movement of both species of snakes. A series of tests was carried out to determine more fully the significance of temperature on the aggregation response. The same aquarium employed in the previous experiment on humidity was utilized again and the humidity was kept constant by the water vapor and calcium chloride apparatus described before. The temperature was controlled by means of an electric heater and all experiments were carried out in a dark room.

The snakes were placed in the aquarium and allowed to remain undisturbed for a period of 15 minutes at a constant humidity and temperature. At

the end of this period the number of individuals in an aggregation was tabulated on a percentage basis. In all cases an aggregation consisted of a group of 3 or more of the total number of snakes.

The results presented in Table 5 show that the greatest percentage of aggregation takes place at temperatures ranging from 21 to 31° C. Below 21° the snakes were sluggish and would remain in any one position for 5 or 6 hours and disturbance of any kind failed to induce reactions. At temperatures above 31 and to 35° C. the snakes appeared irritable and uncomfortable. They would crawl around the side of the cage continuously. When disturbed at these high temperatures they would immediately react to stimulation by aggregation but the aggregates would break up as soon as left undisturbed and the snakes would continue to move about as before. When the temperature rose above 35° C. the snakes were never found in aggregates or moving around. They would usually be found extended along the edges of the cages. Disturbance had no effect at these temperatures.

The above experiments were then repeated on *T. butleri* and similar results were obtained with the exception that aggregation reactions took place at higher temperatures. The highest temperature at which aggregation occurred in this series was approximately 40° in contrast to 35° in *S. dekayi*. The same difference is present at lower temperatures. At 10 to 12° C., *T. butleri* reacted similarly to *S. dekayi* when the latter were subjected to a temperature of 7.2° C. Below 10° C., *T. butleri* failed to aggregate when disturbed.

TABLE 5. The aggregation response in relation to temperature variations.

| Number of Snakes | Trials | Percentage Rel. Humidity | Temperature Centigrade | Percentage Aggregation |
|------------------|--------|--------------------------|------------------------|------------------------|
| 10..... | 3 | 40 | 7.2 | 50 |
| 10..... | 4 | 40 | 10.0 | 50 |
| 10..... | 5 | 40 | 10.0 | 40 |
| 10..... | 5 | 40 | 12.0 | 50 |
| 10..... | 6 | 40 | 15.0 | 40 |
| 20..... | 5 | 40 | 17.0 | 30 |
| 20..... | 6 | 40 | 19.0 | 55 |
| 20..... | 5 | 41 | 21.0 | 75 |
| 10..... | 8 | 40 | 23.0 | 80 |
| 20..... | 6 | 41 | 25.0 | 80 |
| 20..... | 5 | 40 | 27.0 | 95 |
| 20..... | 5 | 40 | 29.0 | 70 |
| 10..... | 8 | 40 | 31.0 | 70 |
| 10..... | 6 | 40 | 33.0 | 40 |
| 20..... | 5 | 40 | 35.0 | 20 |
| 20..... | 5 | 40 | 37.0 | .. |
| 20..... | 6 | 40 | 39.0 | .. |

In connection with the above temperature studies, the maximum temperature tolerance or temperature which would prove fatal to the snakes at a given humid condition was noted in both *S. dekayi* and *T. butleri*. The

average maximum tolerance for 10 *S. dekayi* with the relative humidity at 35 per cent was 41° C. The variations in this group covered a range from 39 to 44° C. The average tolerance for *T. butleri* at 35 per cent relative humidity was 48° C. The variations for *T. butleri* were from 45 to 53° C.

From these studies it may be concluded that aggregation takes place normally within a more or less definite temperature range and that the response to disturbance is more stimulating at certain definite temperatures. Here again, when disturbance factors are introduced they dominate over temperature responses but the response at unfavorable temperatures is very temporary. *T. butleri* forms typical aggregations at higher temperatures than the optimum for *S. dekayi*. Furthermore, the temperature tolerance of the first species is approximately 7° C. higher than that of the second.

THE RÔLE OF THE SENSE ORGANS IN AGGREGATION

Since the aggregation response is quickly evoked in *S. dekayi* even when the snakes are widely scattered about the cage, it is apparent that some distance receptor must play a part in the reaction. In order to determine which receptor or combination of receptors is directly involved in the response, the functioning of the various sense organs was eliminated, as in the humidity experiments, either singly or in combination, and the effect upon the aggregation response recorded.

Vision, olfaction and the tongue were eliminated as previously described. Jacobson's organ was destroyed by cauterization following etherization. The operation was checked by a study of serial sections of the heads of the snakes treated, and the Jacobson's organ was found to be completely destroyed in these cases. The mortality from this operation was less than 10 per cent. No cauterized snakes were used in the tests until two weeks after operation when they were feeding normally.

The snakes to be tested were placed in glass-sided cages measuring 12 x 21 x 14 cm. A layer of slightly dampened gravel was spread over the floor of the cage. Some of the cages were maintained in a photographer's dark room and others in a well lighted room. Aggregation was induced in some cases by either suddenly shaking the cage or merely tapping one of the glass sides. This was continued for a period of 3 minutes and the distribution of the snakes recorded. Since under these conditions there was always a certain amount of shifting and reforming of the aggregations it was only rarely in the controls that all the snakes were found to be aggregated at the termination of the 3-minute period. On the other hand when the snakes were moving at random about the cage a few at any one moment might be temporarily in contact. Hence we have taken an arbitrary standard of 90 per cent of the total number of snakes aggregated as a positive reaction and of less than 20 per cent as negative reaction. In our first series of tests tab-

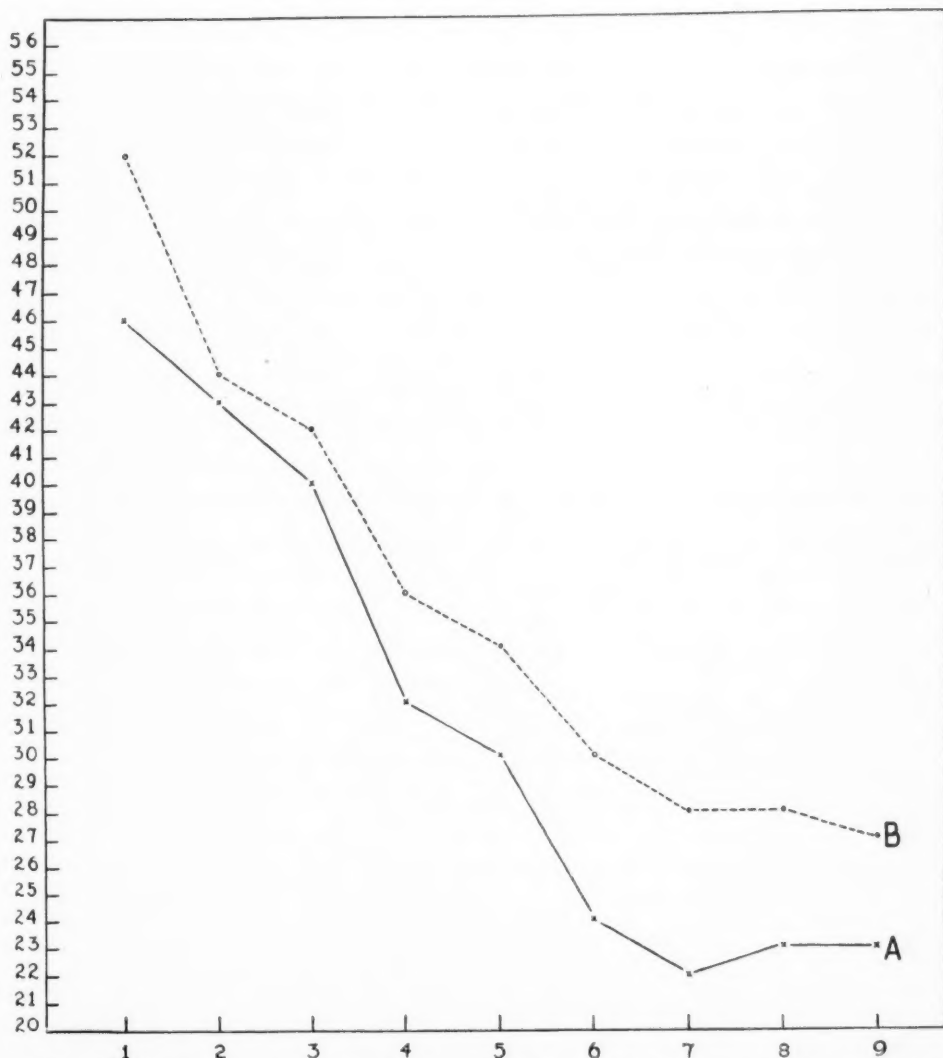


FIG. 7. The average rate of respiration of five *S. dekayi* in an aggregated condition in a container at 30° C. over a 9-hour period in comparison to 5 isolated *S. dekayi* in containers at the same temperature for a similar period, the aggregate being kept dry and the isolated moist. Broken line B, the isolated; continuous line A, the aggregate; abscissas, hourly period; ordinates, respiratory counts per minute.

ulated below, the room temperature was approximately 21° C. The relative humidity was maintained at 45 per cent throughout the entire period of this set of experiments. In Table 6 the same series of abbreviations are employed as have been used in Table 4. These will be employed throughout this paper to indicate snakes with one or more sensory functions eliminated. In each series, under both light and dark conditions, aggregation was induced with the experimental snakes in the same cage with control snakes. The controls were then removed and the same test repeated. In no case, as recorded in Table 6, were the reactions of the experimental snakes affected by the presence of the controls.

From Table 6 it is clear that in the blindfolded series all trials gave definite aggregations. No difference was noted between the light and the dark room series as regards the average time taken for aggregation. It was, however, quite evident that the reaction time was much slower in the cases of this experimental series than for the controls. It required nearly 3 minutes for the experimentals to aggregate while the controls with their unobstructed vision reacted almost instantly. In the nose-stopped series very different results were obtained. The tests made in the dark room gave no aggregation response in contrast to those made in the light room. The two groups were left in the dark room over night, and the following morning 10 of the 14 controls and 4 of the 10 experimentals were found in two clusters

TABLE 6. The influence of sense organs on aggregation.

| *Series | **Room | Number of Snakes | | Trials | Reaction |
|-----------|--------|---------------------------|----------------------|--------|--------------|
| | | Experimental ¹ | Control ² | | |
| B | L | 15 | 0 | 3 | Positive |
| B | L | 15 | 10 | 3 | Positive |
| B | D | 15 | 0 | 4 | Positive |
| B | D | 15 | 10 | 3 | Positive |
| N | L | 14 | 0 | 3 | Positive |
| N | L | 14 | 10 | 3 | Positive |
| N | D | 14 | 0 | 8 | Negative |
| N | D | 14 | 10 | 3 | Negative |
| T | L | 12 | 0 | 4 | Positive |
| T | L | 12 | 10 | 5 | Positive |
| T | D | 12 | 0 | 4 | Positive |
| T | D | 12 | 10 | 4 | Positive |
| BN | L | 14 | 0 | 5 | Negative |
| BN | L | 14 | 10 | 5 | Negative |
| BN | D | 14 | 0 | 4 | Negative |
| BN | D | 14 | 10 | 4 | Negative |
| BT | L | 12 | 0 | 4 | Positive |
| BT | L | 12 | 10 | 3 | Positive |
| BT | D | 12 | 0 | 2 | Positive |
| BT | D | 12 | 10 | 3 | Positive |
| NT | L | 11 | 0 | 3 | Positive |
| NT | L | 11 | 10 | 5 | Positive |
| NT | D | 11 | 0 | 5 | (4) Negative |
| NT | D | 11 | 10 | 5 | Negative |
| BNT | L | 11 | 0 | 4 | Negative |
| BNT | L | 11 | 10 | 4 | Negative |
| BNT | D | 11 | 0 | 3 | Negative |
| BNT | D | 11 | 10 | 4 | Negative |

*Designates type of experimental animal used, i.e., - B, blindfolded; N, nose-stopped; T, tongueless; BN, blindfolded and nose-stopped; BT, blindfolded and tongueless; NT, nose-stopped and tongueless; BNT, blindfolded, nose-stopped and tongueless.

**L - Daylight (in front of window); D - Darkroom.

¹Animals from which sensory structures were removed.

²Untreated animals.

while the remaining 6 experimentals were scattered over the entire cage. Hence it was clear that plugging the nostrils had a very definite effect of delaying, if not preventing, the aggregation response.

In the tongueless series the tongues had been removed from the 12 individuals 5 days before the experimental data were recorded. In this series 17 tests were positive and the snakes all aggregated into 1 or 2 groups. However, the reaction time as recorded tended to be somewhat slower under the dark conditions. In view of the reported importance of the tongue in the sensory life of snakes it was of interest to find that removing the tongue did not prevent the snakes from aggregating in the dark.

In the blindfolded and nose-stopped series all reactions were negative. Of the 18 tests made under both light and dark conditions, as well as in supplementary tests where the snakes were left over night in the dark room, no signs of aggregation were noted. This was also true even though the snakes frequently came in contact with one another while wandering about the cage. They would crawl over one another in the same indifferent way as when coming in contact with sticks or pieces of wood placed in the cage. In this group of blindfolded and nose-stopped snakes the tongue was protruded more rapidly and more extensively than in the controls.

In the nose-plugged and tongueless series the results were very different whether or not the cages were placed in the dark room or in the light. All the daylight tests gave definite aggregation responses while 90 per cent of the dark room tests were negative. The one positive result in the series of 10 trials of the dark room series requires further comment. At the end of the 3-minute stimulation period there were 6 snakes in one cluster, 8 in another and one isolated. These same individuals were left over night in the same cage with 10 controls. In the morning all the controls had aggregated but only 30 per cent of the nose-plugged and tongueless individuals were grouped.

We may conclude from the data listed in the above table that vision and, less extensively, olfaction, are the chief senses which enter into the aggregation response. The tongue plays little or no part in the response. Since the tongue is believed to have important functions in the food seeking reactions of other snakes we may return to the question of the function of the tongue in *Storeria* after we have examined its feeding behavior. So far as aggregation is concerned vision is the chief aid to a rapid response. The question remains nevertheless as to how specific the visual cues must be to evoke an aggregation response.

EXPERIMENTS WITH MODELS AND NARCOTIZED INDIVIDUALS

In order to test whether or not the aggregating snakes were reacting to some external feature which helped to make up the general appearance of the species a series of tests was made with narcotized individuals with whole

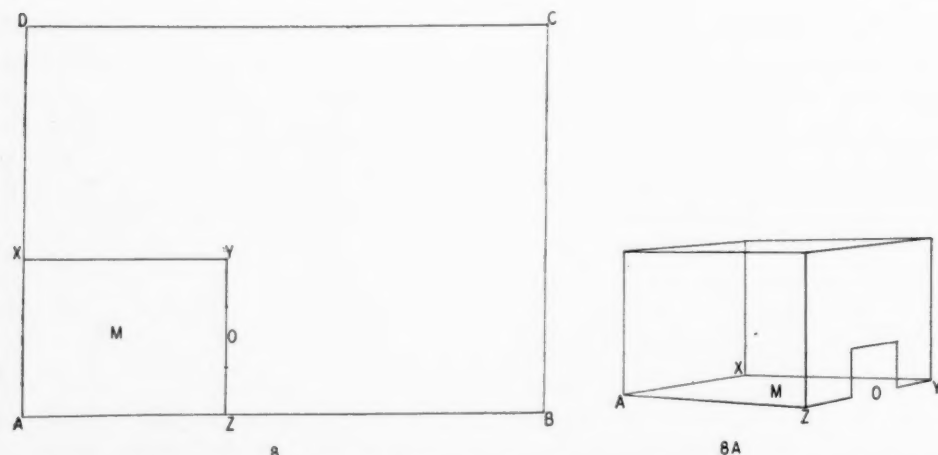


FIG. 8. Diagram showing how the glass plates XY and YZ were arranged at right angles in cage ABCD. M, the region where the aggregate was placed. O, the aperture used in some of the experiments as outlined. 8A, a side view.

specimens infiltrated with paraffin, and with colored wax casts. The casts and the infiltrated specimens were taken from the exhibition hall of the American Museum and represented a very close approximation to the living *S. dekayi*. The narcotized snakes were injected with a 5 per cent solution of cocaine.

Eight normal and 8 other snakes having one or more sensory organs incapacitated were placed in the cages with 5 narcotized snakes or with 5 infiltrated specimens or casts. A reaction was interpreted as positive when at least 5 of the 8 normal or 5 of the 8 experimental snakes remained in contact with the models or narcotized forms for a period of 5 minutes. This was a different criterion of aggregation from that utilized in the previous tests but in view of the fact that the models and narcotized individuals were held motionless during the test the conditions of the experiment were different from those reported above and hence a new criterion of aggregation seemed desirable.

In one series of tests the snakes with functional sense organs were immersed in a 10 per cent solution of magnesium sulphate for the purpose of anaesthetizing the skin. The treatment was repeated with a series having the nostrils plugged, the tongue removed and the eyes blindfolded. It was previously found that this treatment rendered normal snakes more sluggish in all their movements but did not prevent aggregation. It seemed to follow, that in snakes equipped with the eyes, nose and tongue, skin sensibility did not enter into the aggregation response. It nevertheless seemed possible that the tactile organs of the skin might enter into the discrimination of active from quiescent snakes and hence the treatment was repeated on some of the individuals employed in the following experiments. In Table 7 the same ab-

breviations are utilized as above. In addition "U" refers to the untreated individuals having all their sense organs intact and "A" to the series with anaesthetized skin.

The tests as tabulated above demonstrate that *Storeria* will not aggregate with quiescent individuals of the same species whether these be narcotized individuals or infiltrated specimens or models. Whether this is due to a lack of reciprocal movement on contact or to the lack of bodily movement before contact is not brought out by these particular tests. Tongueless *Storeria* reacted exactly like the intact controls. Over the entire series of tests where the nostrils were closed the results were quite diverse. In 66 per cent of these cases the experimentals aggregated with the models and the narcotized individuals. Forty-two per cent of this series reacted positively under dark room conditions. This indicates that vision plays some part in the process of differentiation between live forms and models or narcotized forms. Since there was only a 3 per cent difference in the response to the narcotized indi-

TABLE 7. Aggregation with models and narcotized forms.

| Series | Trials | With Models | | | | With Narcotized Forms | | | |
|------------------------|--------|-------------|---|----------|---|-----------------------|---|----------|---|
| | | Daylight | | Darkroom | | Daylight | | Darkroom | |
| | | + | — | + | — | + | — | + | — |
| U | 10 | | — | | — | | — | | — |
| B | 10 | | — | | — | | — | | — |
| T | 10 | | — | | — | | — | | — |
| BN | 16 | 3 | 1 | 4 | — | 2 | 2 | 4 | — |
| N | 16 | | — | 2 | 2 | | — | 2 | 2 |
| NT | 16 | | 4 | 3 | 1 | 1 | 3 | 3 | 1 |
| BNT | 20 | 4 | 1 | 3 | 2 | 3 | 2 | 5 | — |
| BT | 10 | | — | | — | | — | | — |
| A ¹ | 15 | | — | | — | | — | | — |
| BNT ¹ | 18 | 2 | 3 | 2 | 2 | 4 | 2 | 1 | 2 |

¹Abbreviations as in Table 6. In addition to these—

U, Untreated. A, Skin anaesthetized with 10 per cent magnesium sulphate.

viduals compared to that of the models it would appear that when the nostrils are closed *Storeria* is unable to discriminate between them in the dark.

EXPERIMENTS WITH GLASS PLATES AND MIRRORS

In the aggregation response of *Storeria* vision appears to play a dominant rôle but as shown above the snakes will not aggregate with narcotized individuals or with models. They also do not respond to freshly killed individuals. Hence it is apparently the movement of some of the snakes in any one group which calls forth the aggregation response. In order to test this conclusion we devised another series of experiments.

In the first experiments a group of intact *Storeria* was separated from others in the cage by means of a glass plate partition. Figure 8 shows how

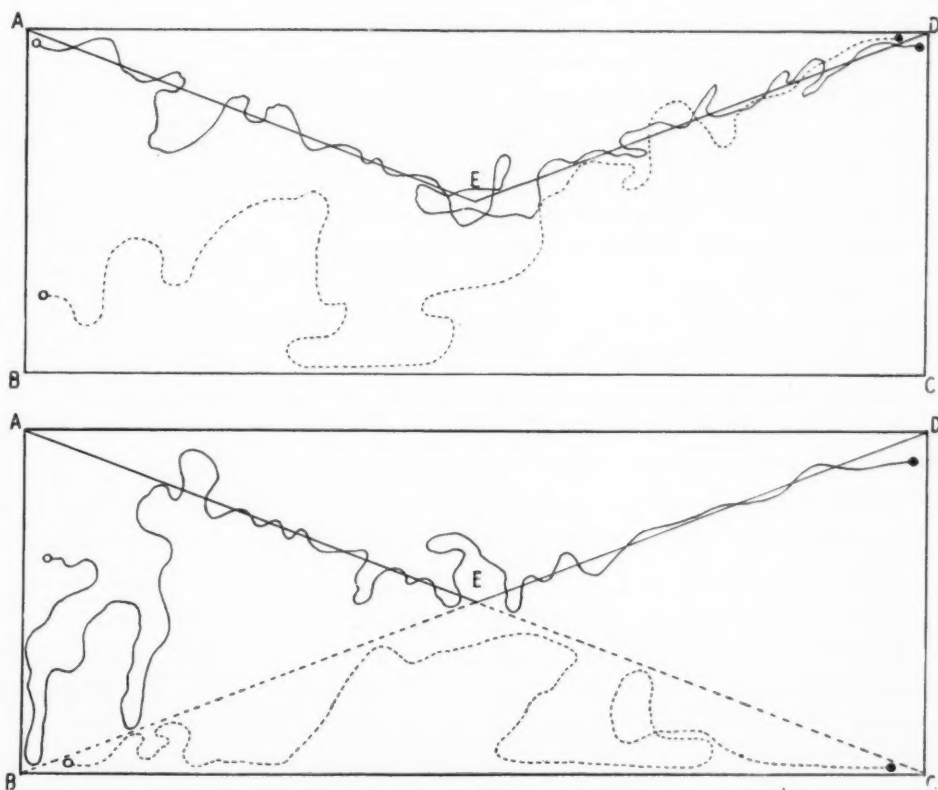
the glass was placed in the cage. Two glass plates, XY and YZ, were arranged at right angles in one corner of the cage. A cluster of snakes was then placed in the region M. A similar number of snakes was distributed in the area YC. The snakes in region YC were then disturbed and all but a very few of them invariably moved to the aggregation already formed in region M enclosed by the glass plates. This test was repeated 10 times and an average of 80 per cent of the total number of snakes in region YC moved toward the aggregate M. These moving snakes made deliberate efforts to pass through the glass plates toward the aggregation. They would run into the glass and then move along the sides of the plate and in some cases attempted to crawl up over the plates.

All the snakes in both region M and YC were then blindfolded. The individuals in region M were allowed to aggregate first and the snakes in area YC were disturbed as previously. Instead of moving toward the already formed cluster in region M, they aggregated within their own group in region YC. No attempts were made to pass through the glass plates to region M. When these snakes were only nose-stopped, reactions were exactly the same as in the normal series in the daylight. However, nose-plugged snakes, when placed in a dark room failed to move towards the glass partition and only about 40 per cent of each group aggregated within their own region.

In the next series of this group of experiments a square 5 x 5 cm. was left clear in the glass plate XY, and the remainder of the glass plate XY, as well as all of YZ, was covered with black paper.

Figure 8A shows a side view of the right angle partition indicated in Figure 8. In this experiment the snakes were again placed in M and YC. When the normal snakes in YC were disturbed they tended to aggregate into one cluster unless one of the group happened to see the cluster in M through the clear glass O. In this case the individual would move in the direction of O. In 6 out of 12 trials the snakes in area YC aggregated in front of O, the clear portions of the glass XY. In no case did the animals attempt to crawl up the darkened portion of the glass plates but frequently ran against the clear area O.

In the next series of experiments, instead of employing a glass partition, a cardboard of the same size as XY was substituted. In this partition an opening of the same size as aperture O was cut. The cardboard was colored black, and the snakes utilized in the preceding experiment were tested in this apparatus. In these tests the normal snakes all passed through the opening O without attempting to form an aggregate outside of the aperture. The tests were then repeated on blindfolded animals with the result that they all passed through the opening in the same manner as the normals but more slowly. When a series of nose-stopped individuals was substituted for the blindfolded and the tests repeated in the daylight, the movements were exactly



FIGS. 9 and 10. Figure 9 shows the trails of two male *S. dekayi* starting at AB and ending at D. Trail AED was made by rubbing body integument over the course. Figure 10 shows the same two male snakes beginning at AB. AED scented with body integument. Trail BEC scented with cloacal gland secretion.

the same as for the normals in the daylight. When the apparatus was shifted into the dark room no snakes passed through aperture O. The entire series responded similarly to the blindfolded, nose-stopped individuals.

Although the above experiments clearly indicated the importance of vision and the secondary rôle of olfaction in the aggregation response these conclusions were tested further by means of mirrors. When a *Storeria* with all the sense organs intact was placed in a cage containing a mirror it would almost invariably come to rest in front of the mirror. If the position of the mirror was changed and the snake disturbed it would move with some rapidity to the side of the mirror and would remain there for several hours if left undisturbed. It would seem from this experiment that the attraction of a mirror for a disturbed snake was almost as great as the presence of another snake. Further tests, however, disclosed a difference, for when groups of *Storeria* were placed in the cage containing the mirror, the snakes did not always aggregate in front of the mirror. Out of 15 such trials, 8 cases of 100 per cent aggregation occurred in front of the mirror. In the other 7

trials 1 or 2 of the snakes were found in front of the mirror while the main cluster was gathered in another region of the cage.

Two mirrors were then placed at right angles to one another in one corner of the cage. One snake was then placed in the cage and disturbed. The snake would invariably move up in front of one of the mirrors. Two snakes were then placed in the cage, one of them being placed in front of each of the mirrors. When disturbed they would always aggregate in one cluster regardless of the images in the mirror. It follows from these experiments that an active *Storeria* is a greater attraction to another than the mirror image of either one.

When this test was repeated with a normal *Storeria* and an infiltrated model the normal snake reacted indifferently to the model in 75 per cent of the cases but would make contact with the mirror. In the other 25 per cent of the cases it aggregated with the model. The model was then removed and a stick of wood or a piece of rubber tubing substituted. The results were the same as for the model.

When the infiltrated specimen was removed and a group of blindfolded *Storeria* was placed in front of the double mirror the snakes again aggregated among themselves as in the case of the normals and not with the mirror images. All of the above experiments with the right angle mirror were carried out in the daylight. When this series of tests was repeated in the dark room no aggregation against the mirror occurred in any case.

It seemed possible that a *Storeria* might prefer an active snake to its own image merely because the active snake was moving differently from itself. We have tested this question by another series of tests. A mirror was fastened at either end of the cage and a group of normal *Storeria* was placed in the mid-region and disturbed. In over 20 such tests the results gave no evidence of a difference as regards regional preference. That is, approximately 50 per cent aggregated at either end or the majority would aggregate at one or the other ends of the cage approximately the same number of times. Then glass plates were substituted for the mirrors and a single snake placed behind each one. When a pair of snakes was placed before the glass plates which were held at right angles to one another, the two snakes would move together to make contact and did not attempt to aggregate with the snakes behind the glass. Hence a snake behind a glass plate is no more attractive to another than is the mirror image of the latter. We ruled out any effect which the texture of the glass might have on the *Storeria* by performing a supplementary series of experiments in which the mirror was placed behind a glass plate. This did not modify the results in any way.

The above experiments with mirrors and glass plates clearly indicate that while vision is of great importance in aggregation the response is more vigorous when aided by some other factor. The experiment with the nose-stopped

series indicates that this secondary factor is olfaction. Since normal *Storeria* attempt to aggregate with other active individuals behind glass we have further evidence of the primary importance of vision in the response.

THE RÔLE OF COLOR IN AGGREGATION

Most species of snakes are distinguished by a particular color pattern which is not found in any other forms. The four species utilized in this study are readily identifiable by color pattern alone. There is frequent reference in the natural history literature to the color pattern of vertebrates as aiding species in identifying their own kind. Since vision plays the most important rôle of color in the aggregation response of *Storeria* it seemed desirable to test the rôle of color in species identification.

A series of *Storeria dekayi* and *Thamnophis sauritus* was selected and 3 individuals of both species were dyed green by using a dilute solution of mercurochrome. The same number of each species was stained blue by using 1 to 10 per cent solutions of methylene blue. The same number was stained red by painting with a 1 per cent aqueous solution of eosin, and yellow by using a saturated solution of chrome yellow. None of the above stains seemed to irritate the snakes which reacted in the normal manner when the dye was dry. These stains did not entirely remove the original color pattern but in all cases the stain, when applied uniformly over the entire body, would change the pattern by obscuring certain elements.

A group of 3 to 5 *S. dekayi* was placed in a cage with a group of painted snakes. The snakes were then disturbed as in the previous experiments and the number of snakes aggregating after a 3-minute interval was recorded. It will be noticed in the following table that *S. dekayi* when provided with its complete sensory equipment will aggregate as readily with individuals of its own species colored bright yellow, blue, red or green as it did previously with uncolored individuals. On the other hand, *S. dekayi* will not aggregate with *T. sauritus* when the latter is stained with the same dyes. The 10 per cent amount of contact recorded in Table 8 falls within the limits of chance contact in any group of non-aggregating snakes. It will be noticed from the table that plugging the nostrils (N series) greatly lowers the amount of aggregation within the *Storeria* snakes during the 3 minute period. Further, the same operation increases the amount of aggregation between *S. dekayi* and *T. sauritus* during the same period.

The above color pattern experiments therefore show that while vision plays an important part in aggregation, the olfaction is also to be considered as an important sensory factor in this behavior. It can also be noted above that color pattern identification in respect to species recognition is not of primary importance but that olfaction is again a dominating sense in this respect.

TABLE 8. Color pattern variations and aggregation.

| Species | Colored Snakes | | Test Snakes <i>S. dekayi</i> | | Trials | Percentage Aggregation |
|--------------------------|----------------|--------|------------------------------|------|--------|------------------------|
| | Number | Color | Number | Kind | | |
| <i>S. dekayi</i> | 3 | Yellow | 3 | U | 4 | 100 |
| <i>S. dekayi</i> | 3 | Blue | 3 | U | 4 | 100 |
| <i>S. dekayi</i> | 3 | Red | 3 | U | 3 | 85 |
| <i>S. dekayi</i> | 3 | Green | 3 | U | 3 | 90 |
| <i>S. dekayi</i> | 3 | Yellow | 3 | B | 4 | 90 |
| <i>S. dekayi</i> | 3 | Red | 3 | B | 3 | 100 |
| <i>S. dekayi</i> | 3 | Blue | 3 | B | 3 | 90 |
| <i>S. dekayi</i> | 3 | Yellow | 3 | N | 3 | 50 |
| <i>S. dekayi</i> | 3 | Blue | 4 | N | 4 | 40 |
| <i>S. dekayi</i> | 3 | Red | 4 | N | 3 | 35 |
| <i>T. sauritus</i> | 3 | Yellow | 4 | N | 5 | 20 |
| <i>T. sauritus</i> | 3 | Green | 4 | N | 4 | 30 |
| <i>T. sauritus</i> | 3 | Yellow | 3 | U | 5 | 10 |
| <i>T. sauritus</i> | 3 | Yellow | 4 | B | 4 | 10 |
| <i>T. sauritus</i> | 3 | Yellow | 4 | NT | 4 | 25 |
| <i>T. sauritus</i> | 3 | Red | 5 | NT | 3 | 20 |

SPECIES IDENTIFICATION IN AGGREGATION

If a series of *S. dekayi* and of *T. sauritus* are placed together in a cage the two species will separate out and each will form one or more aggregations distinct from those of the other species. If an individual of either species is gently placed within the aggregation of the other species it will not remain there but will soon seek its own kind. When the aggregations are left undisturbed for long periods, individual snakes which have freed themselves from the clusters may be seen to make contact with the aggregations of the other species but they rarely, if ever, settle down to remain in contact with these foreign aggregations. In brief, there is a well-marked species factor in the aggregation response.

The previous experiments with colored snakes indicated that olfaction functioned to a large extent in species identification. In order to test this function further a series of *S. dekayi* and another of *T. sauritus* were blindfolded, other series had the nostrils plugged or the tongue excised as in previous experiments. Then a group of snakes including both species was mixed and placed together in a cage. After a 3-minute period of disturbance the amount of aggregation within each species and between the species was recorded. The results are tabulated in the following columns (Table 9).

The table shows that when the two species are only blindfolded or only nose-stopped there is no great decrease in the percentage of aggregation during the 3-minute period. An elimination of both olfaction and vision enormously decreases the percentages of aggregation within the species. This is merely confirmation of results obtained in previous tests. Of special interest was the fact that in all cases where the nostrils were plugged in both species

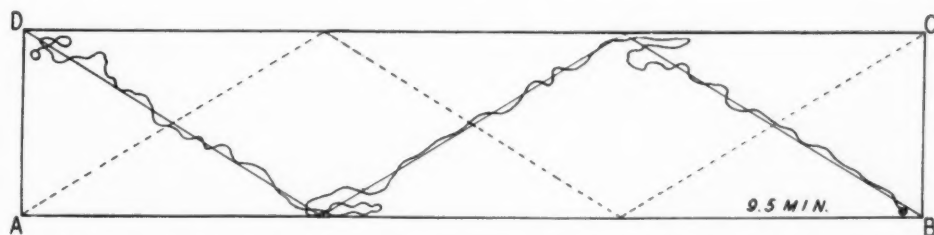


FIG. 11. Trail of normal *S. dekayi* beginning at D and ending at B with the time required to cover the trail.

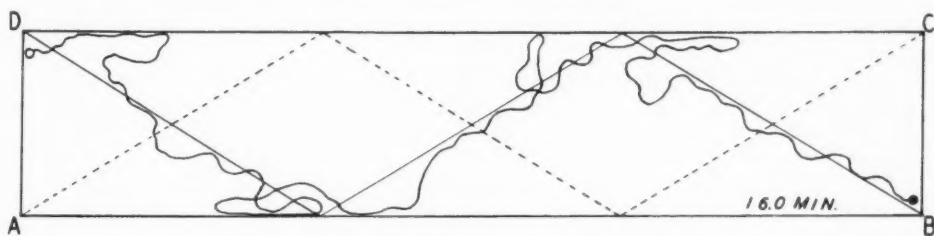


FIG. 12. The trail of an untreated *T. sirtalis*.

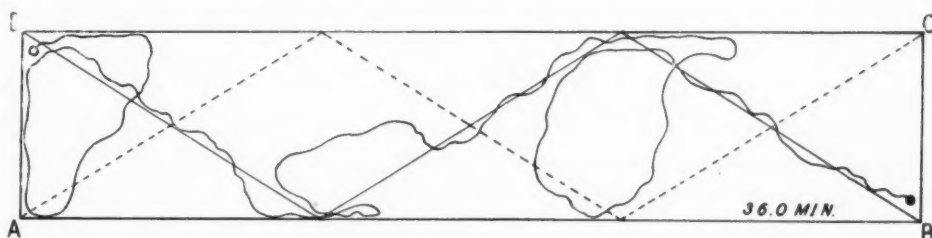


FIG. 13. The trail of an *S. dekayi* with olfaction eliminated.

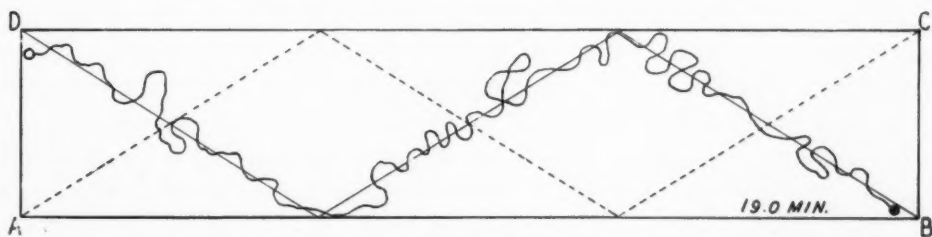


FIG. 14. The trail of an *S. dekayi* with Jacobson's organs incapacitated.

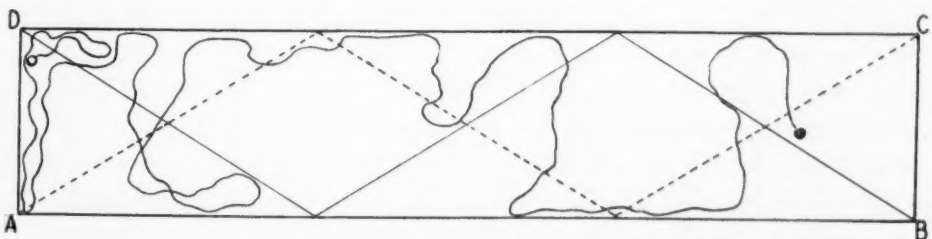


FIG. 15. The trail of an *S. dekayi* with both Jacobson's organs and the olfactory organs incapacitated. No time reaction is listed here since the trail was not followed from D to B and the time involved here was not significant.

FIGS. 11-15. Diagrams of soapstone surfaces. Continuous line in the area, the food scented trail; broken line, the distilled water trail.

TABLE 9. Inter-species identification experiments.

| <i>S. dekayi</i> Series A | <i>T. sauritus</i> Series B | Number of Snakes in Series | | Number of Trials | Percentage Aggregation | | |
|------------------------------|--------------------------------|-------------------------------|---|------------------------|------------------------|-----|----|
| | | A | B | | A | B | AB |
| U | U | 10 | 6 | 5 | 80 | 100 | 0 |
| U | B | 10 | 6 | 4 | 90 | 100 | 0 |
| B | U | 10 | 6 | 3 | 80 | 80 | 0 |
| B | B | 10 | 6 | 4 | 70 | 80 | 0 |
| B | N | 10 | 6 | 4 | 80 | 65 | 0 |
| NT | U | 5 | 4 | 7 | 72 | 82 | 0 |
| NT | NT | 5 | 3 | 8 | 68 | 85 | 25 |
| N | N | 8 | 6 | 4 | 60 | 72 | 35 |
| BN | BN | 8 | 6 | 4 | 45 | 55 | 50 |
| BNT | BNT | 8 | 6 | 5 | 35 | 45 | 40 |
| T | T | 6 | 5 | 4 | 90 | 90 | 0 |

a certain percentage of aggregation between the species occurred. When the tongue alone was removed no aggregation between the species took place. This would indicate that the tongue plays no part in species identification.

THE SIZE FACTOR IN AGGREGATION

It has been shown in the preceding experiments that a snake will not aggregate with another species if its olfactory functions are unimpaired. Conversely, when the nostrils of two species were plugged, the percentage of aggregation greatly increased. In nature snakes frequently show very little of their bodies when crawling through the grass or other cover. This, therefore, raises the question of whether a small portion of the body of another species would serve as a source of attraction if odor was excluded. Before attempting to answer this question it seemed important to establish the amount of a snake's body which would attract individuals of its own species.

To establish this point a glass tube 15 cm. in length and 4 cm. in width was sealed at one end and fitted with a tight rubber stopper at the other. After inserting a DeKay's snake within the tube the outside of the tube was wrapped with a strip of black paper 1 cm. in width. The paper was wrapped in such a way that it could be slipped back and forth on the tube, exposing various portions of the enclosed snake. The tube was then suspended about 1 cm. above the gravel floor at one end of the cage and a similar tube containing no snake was suspended in a like manner at the other end of the cage. Another DeKay's snake was placed in the cage midway between the two tubes and the movements of this snake recorded with respect to the enclosed snake and the control tube. The position of the glass tubes was frequently changed but data recorded in Table 10 were taken for only a single position because the length of time required to make contact with the tube naturally varied with the distance of the snake from the tube.

It will be noted in the following table that a *Storeria* will come in contact with the glass tube when only 40 mm. of the enclosed snake's body is exposed. When this area is reduced to 10 mm. in length no aggregation response will occur. At least in 5 trials the free snake never came to rest in contact with the glass tube having 10 mm. of the enclosed snake's body exposed to view. A blindfolded *Storeria* will not respond even though all of the enclosed snake's body is exposed. When the *Storeria* within the glass was stained yellow or blue the free snake with unobstructed vision made contact with the tube in the average time of one minute even though only 150 mm. of the tube snake was visible.

When a *T. sauritus* or a *T. sirtalis* was placed in the tube and sealed the same aggregation response was induced in the free *Storeria* as when another *Storeria* was within the tube, but the time required for the response was greater. In other words in the absence of odor *Storeria* will attempt to aggregate with a foreign species but more slowly than it would with its own kind in the tube. It is possible that this time difference is due to the fact that all adult *Storeria* have reacted so frequently toward their own species that they are, to a certain extent, conditioned. However, our experiments have not been sufficiently numerous to determine what influence, if any, learning has on the aggregation response.

TABLE 10. The visual response in respect to the size of the object.

| Tube Snake | | Exper. Snakes | | Mm. of Tube Exposed | Trials | Reaction | Reaction Time (sec.) |
|----------------------------|----------|---------------|-----------|---------------------------|--------|------------|----------------------------|
| Species | Size mm. | Number | Condition | | | | |
| <i>S. dekayi</i> | 150 | 1 | U | 150 | 3 | Positive | 45 |
| <i>S. dekayi</i> | 150 | 1 | U | 75 | 2 | Positive | 110 |
| <i>S. dekayi</i> | 150 | 1 | U | 40 | 4 | Positive | 120 |
| <i>S. dekayi</i> | 150 | 1 | U | 10 | 5 | Negative | ... |
| <i>S. dekayi</i> | 150 | 1 | B | 150 | 3 | Negative | ... |
| <i>S. dekayi</i> | 150 | 1 | B | 15 | 2 | Negative | ... |
| <i>S. dekayi</i> * | 150 | 4 | U | 150 | 3 | 1 Positive | 240 |
| <i>S. dekayi</i> | 150 | 4 | U | 75 | 3 | Positive | 300 |
| <i>S. dekayi</i> | 300 | 1 | U | 150 | 3 | Positive | 40 |
| <i>S. dekayi</i> | 300 | 1 | U | 75 | 2 | Positive | 60 |
| <i>S. dekayi</i> | 300 | 4 | U | 150 | 3 | Positive | 180 |
| <i>S. dekayi</i> | 300 | 4 | B | 150 | 4 | 2 Negative | ... |
| <i>S. dekayi</i> ** | 200 | 1 | U | 150 | 3 | Positive | 60 |
| <i>S. dekayi</i> *** | 200 | 1 | U | 150 | 3 | Positive | 60 |
| <i>T. sauritus</i> | 300 | 1 | U | 150 | 3 | Positive | 60 |
| <i>T. sauritus</i> | 300 | 1 | U | 75 | 3 | Positive | 115 |
| <i>T. sauritus</i> | 300 | 4 | U | 100 | 3 | Negative | ... |
| <i>T. sirtalis</i> | 270 | 1 | U | 150 | 5 | Positive | 90 |
| <i>T. sirtalis</i> | 270 | 4 | U | 150 | 4 | Negative | ... |

*One snake went to tube snake in 3 trials. **Tube snake colored yellow. ***Tube snake colored blue.

It will also be noted from the above table that when several snakes are placed in the cage together at some distance from the tube they will attempt to aggregate among themselves and not with the snake in the tube. This

seems to indicate that when odor is present to facilitate any impulses derived from optic stimulation, the response is towards the source of this double stimulation.

The experiments summarized in the above table show that while the visual impression serves as a source of attraction during aggregation the species identification is accomplished primarily by some other receptor mechanism. Since *Thamnophis* will attract *Storeria* when sealed in a glass tube it would seem highly probable that species identification is accomplished primarily by odor.

THE RELATION OF AGGREGATION TO EFFORTS AT CONCEALMENT

As stated in the earlier paragraphs of this report the aggregation response of the extreme type employed to some extent in this study is far less commonly seen in nature than a less vigorous response which leads one individual to seek others of its kind when these are hidden. *S. dekayi* will readily bury itself in the dry gravel on the floor of the cage but in doing so it will usually seek the same part of the cage already occupied by others of its species. If a group of snakes were already concealed, vision would not enter at all into the response. Such behavior appears at first more like an attempt to reach suitable cover than to aggregate. It seemed desirable to treat the sense organs entering into this response with a view to throwing further light on the nature of the reaction.

Early in our experiments it was found that *Storeria*, when placed in a glass-sided cage employed in this study, would endeavor to hide beneath a cross piece of wood which held down the gravel filled tray of the cage. When several snakes were placed together in the cage they would frequently soon begin to disappear under the gravel at this end of the cage. This attempt at concealment was observed several times and in no series of cases did a particular individual assume leadership in the "march" toward the cross piece. The snake nearest the bar usually took the lead and was then followed by the remainder of the group. When the frame was completely covered with gravel the snakes would burrow through it in an effort to hide. When a hole was made in the gravel under the cross piece, this aperture was always selected by the first snake to reach it and the other snakes followed the leader down the hole, the group spreading out under the cross piece. The time required for the first snake to enter and completely conceal itself was approximately twice that taken for the second to complete the same process when both were the same distance from the bar. Records were kept of the time required for the complete concealment of 10 individuals over a series of 6 trials. The average time was 4 minutes at a temperature of 24° C. However, at a lower temperature of 13° C. the average time required was 6.2 minutes over a series of 7 trials. The same experiments were carried out in the dark room and in a

series of 5 trials the average time for complete concealment was 9.1 minutes at 24° C.

A series of *S. dekayi* having the eyes blindfolded, the nostrils plugged or the tongues excised was used and the time required to enter the hole under the cross piece recorded. The experiment was run at 28° C. under both dark and light conditions. Table 11 records the results of the above experiment. These experiments show that vision is the primary functional sense organ used by one *Storeria* when placed in a cage and required to find the aperture leading under the cross piece under which another *Storeria* has previously been placed. However, olfaction also is functional since there is a difference in time required for concealment of the nose-stopped snake as compared with the untreated. When vision and olfaction are both eliminated as in the case of the nose-stopped series under dark conditions the snake in all cases failed to enter the aperture.

TABLE 11. Speed of concealment in relation to the sense organs involved.

| Series | Room | Individual Trials (Time in min.) | | | | | | Average Time* |
|-----------|-------|----------------------------------|------|------|------|------|-----|---------------|
| | | | | | | | | |
| U | Light | 3.5 | 3.0 | 3.0 | 4.5 | 5.0 | 5.5 | 4.0 |
| B | Light | 10.0 | 12.0 | 10.5 | 11.0 | 12.0 | ... | 11.1 |
| N | Light | 7.0 | 5.5 | 5.0 | 6.5 | ... | ... | 6.0 |
| N | Dark | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| T | Light | 4.0 | 4.5 | 4.5 | 5.0 | 3.5 | ... | 4.2 |
| T | Dark | 12.0 | 9.5 | 11.5 | 10.0 | 10.0 | ... | 10.2 |
| BNT | Light | 0.0 | 0.0 | 0.0 | 0.0 | ... | ... | 0.0 |

*All tests carried out at room temperature, 24° C.

At the conclusion of this series of tests the gravel on the floor of the cage was thoroughly moistened with water. The tests were then repeated in both the light and dark. Only about 30 per cent of the *Storeria* which had entered the hole under the cross piece previously would repeat this response when the gravel was thoroughly moistened. Moreover, the time required was 3 to 4 times longer. Turning the cages at various angles to the light did not affect the results.

The degree of moisture has, therefore, a marked influence on the efforts of *Storeria* toward concealment by burrowing. By introducing blocks of wood of various sizes in the cages it was found that the size of the block also has an influence since fewer snakes will cluster under the smaller than under the larger blocks. The presence of a hole leading under the block is not an essential requirement. Once a snake is concealed below a block of wood placed anywhere in the cage this block becomes more attractive than any other similar block in the same cage. The question was raised as to whether olfaction or some other sense was employed to find these completely hidden snakes. To answer this question a new series of tests was devised.

A series of *S. dekayi* was placed in cages containing very dry gravel but no moss. The temperature was 26° C. and relative humidity 20 per cent. Under these conditions the snakes would always seek cover. The end cross piece of the cage in the absence of other blocks, offered a means of retreat. One snake was placed in the cage and it would move to this end of the cage and burrow through the gravel to work its way under the cross piece. When this snake had completely concealed itself, the hole it had made in the gravel was smoothed over and another snake placed in the cage and its movements observed. This snake would move in the same direction, and in 90 per cent of the cases would burrow through the gravel in the same region as the first. This was repeated for 3 more snakes with the same result. The experiment was then repeated with snakes having one or more sense organs incapacitated. We have included in these tests, snakes with Jacobson's organs destroyed by cauterization. The data recorded in the last column of Table 12 give the average time required for the third snake of the series of 5 snakes in each series of trials to burrow out of sight near the two snakes which had been released previously one after the other.

TABLE 12. Concealment following the elimination of particular sense organs.

| Series* | Trials | Reaction | Percentage | Time in Seconds |
|------------|--------|----------|------------|-----------------|
| U | 8 | Positive | 90 | 150 |
| T | 5 | Positive | 80 | 175 |
| B | 7 | Positive | 85 | 240 |
| BT | 7 | Positive | 72 | 310 |
| BN | 9 | Positive | 12 | 720 |
| NT | 8 | Positive | 20 | 520 |
| BNT | 12 | Positive | 16 | 630 |
| N | 9 | Positive | 12 | 600 |
| BNJ | 10 | Positive | 10 | 830 |
| BNJT | 10 | Negative | .. | ... |
| BJ | 10 | Positive | 80 | 205 |
| NJ | 10 | Positive | 10 | 900 plus |

*Usual series abbreviations with the addition of J, which designates the removal of Jacobson's organs.

This series of experiments shows that in any series of tests where the olfactory sense is incapacitated the reaction is either entirely or partially disrupted. The trailing is accomplished chiefly by olfaction, with the tongue and Jacobson's organ functioning as secondary recipient structures.

THE NATURE OF THE OLFATORY STIMULUS TO AGGREGATION

Although it has been shown in the preceding experiments that olfaction plays a part in aggregation and is the chief sensory mechanism for discriminating between species, no attempt was made above to localize the source of the odor to a particular part of a snake's body. It is well known that snakes are provided in both sexes with cloacal glands which produce a highly odorous substance having frequently a distinctive color and usually a de-

detectable difference in odor in the different species. It is no wonder that many naturalists such as Prater (1933) have suggested that one of the functions of these glands is to help a species in finding its own kind. However, we have never seen even the blindfolded snakes, when aggregating, seek the cloacal region of another snake in preference to some other part of the snake's body. Hence it seemed desirable to determine by experiment if one part of a snake's body is more attractive than some other part to an aggregating snake.

When a blindfolded *Storeria* was placed in one end of a cage and a blindfolded, nose-stopped individual at the other, it was noticed that the former moved to the end containing the latter. The blindfolded, nose-stopped snake was removed and its cloacal region carefully covered with adhesive tape and then covered with vaseline. When replaced in the cage it moved to within 4 cm. of the blindfolded one. The latter immediately moved forward to bring its body in contact with the taped snake. The blindfolded snake was then removed and a blindfolded tongueless individual substituted. This snake, like its predecessor, soon aggregated with the taped snake. The latter being both blindfolded and nose-plugged, moved about the cage aimlessly. When it came within 5 to 7 cm. of the blindfolded and tongueless snake the latter was stimulated to move toward the taped snake and aggregate with it.

The blindfolded and nose-plugged snake was next thoroughly washed with soap and water and its cloacal region sealed as before with vaseline. The experiments with the blindfolded and the blindfolded and tongueless *Storeria* were repeated with similar results. The washing had not removed the source of attraction because both blindfolded and blindfolded, tongueless snakes would seek out the taped snake. However, the attraction appeared to be weaker because there was considerable moving about before the snakes settled down to form an aggregation.

The blindfolded and nose-plugged snake was then removed and its entire body covered with a thin layer of vaseline. When replaced in the cage with the blindfolded and the blindfolded, tongueless snakes it failed to call forth the aggregation response in these snakes. An infiltrated specimen of *S. dekayi* was placed in the cage to serve as a basis of comparison. The blindfolded and the blindfolded, tongueless snakes showed no more interest in the vaselined snake than they did in the motionless infiltrated specimen.

The experiment was repeated with 3 blindfolded and nose-stopped *Storeria* which had been covered with vaseline. When an untreated *Storeria*, a blindfolded, nose-stopped snake and a blindfolded, tongueless snake were added to the cage there was no aggregation with the vaselined snakes. At the end of a 30-minute period the blindfolded, tongueless and the blindfolded, nose-stopped as well as the untreated *Storeria* had clustered into a single group while the 3 vaselined snakes were isolated in 3 different parts of the cage.

These experiments indicate that the cloacal glands of *Storeria* do not

produce the substances which serve as the basis of attraction during aggregation in the dark. The experiments with the vaselined snakes suggest that integument of the body is the source of these odorous substances. This seems the more remarkable in that there are no glands in the general integument of the body. However, the conclusion is in agreement with the findings of Noble (1936) that the body integument and not the cloacal glands leave a trail which aids snakes in seeking and identifying the opposite sex.

TRAILING EXPERIMENTS

In the preceding series of tests it has been concluded that the body integument and not the cloacal glands, leaves the trail by which snakes seek or find one another. In view of the above conclusions it seemed of importance to carry out a series of trailing experiments to determine the sense organs involved and to elucidate the nature of the stimulus.

The first series of experiments was carried out during the months of November and December 1933. A series of normal *S. dekayi* as well as a series of blindfolded snakes was used in this experiment, also two series in which the snakes were blindfolded and either tongueless or nose-stopped. Trails were made by rubbing the cloacal regions of the body of a snake of the same species over a smooth surface or by rubbing body integument exclusive of the cloacal region over the same surface. The sex of the trailing snake was recorded as well as the sex of the snake with which the trail was made. The experiments were carried out on gravel, concrete and Alberene stone surfaces. The experiments as recorded in Table 13 were all carried out on an Alberene stone surface 70 x 160 cm. The trail was made on exactly the same place and the trailing animal was started at the same place each time throughout the entire series. The table was cleaned with soap and water after each experiment. Table 13 gives the sex of the trailing animal, the sex of the snake with which the trail was scented and the time taken for each trailing animal to cover the trail.

It can be seen from the above table that there is no sexual attraction. A male *Storeria* will follow a male trail as well as a female trail and vice versa—the female will follow a female trail as well as a male trail. This series of experiments also shows that the snake with its sense of vision incapacitated reacts in a normal manner in following the scented trail. In the blindfolded series the reaction time is slightly less than in the untreated series. This is possibly because the experiment was carried out in a lighted room and snakes having their visual sense functional reacted to influences other than the trailing factor. Nevertheless, it can be clearly noted from these results that olfaction is the chief sensory modality for finding and following or avoiding the trail.

Figure 9 shows the trails of 2 males started at various regions at AB and ending at region D on the trail AED, made by rubbing the body integument of

TABLE 13. The sense organs involved in trailing.

| Series | Trials | Sex | Trail Scent | Reaction Time |
|----------|--------|--------|-------------|----------------|
| U | 5 | Male | Male B | 3 min. 10 sec. |
| U | 5 | Female | Male B | 3 min. |
| U | 4 | Male | Female B | 4 min. 10 sec. |
| U | 3 | Female | Female B | 3 min. 40 sec. |
| U | 8 | Male | Male C | Negative |
| U | 5 | Male | Female C | Negative |
| U | 3 | Female | Female C | Negative |
| U | 4 | Female | Male C | Negative |
| B | 5 | Male | Male B | 2 min. 20 sec. |
| B | 4 | Male | Female B | 3 min. 12 sec. |
| B | 3 | Female | Male B | 2 min. 50 sec. |
| B | 6 | Female | Female C | Negative |
| B | 5 | Male | Female C | Negative |
| BT | 5 | Male | Male B | 3 min. 25 sec. |
| BT | 5 | Male | Female B | 2 min. 30 sec. |
| BT | 3 | Female | Female B | 3 min. 45 sec. |
| BT | 5 | Male | Male C | Negative |
| BT | 4 | Female | Male C | Negative |
| BN | 6 | Male | Male B | Negative |
| BN | 7 | Female | Female B | Negative |
| BN | 3 | Female | Male C | Negative |
| BN | 4 | Female | Female C | Negative |

C designates scent from cloacal glands. B designates scent from other body regions.

a male over the course. Figure 10 shows the same 2 males started at AB. In this case AED was again scented with body integument exclusive of the cloacal region while trail BEC was scented with cloacal gland secretion. This figure, as well as the results in the previous table, again substantiate the previous conclusions regarding the nature of the olfactory stimuli. The snakes not only fail to follow a cloacal scented trail, but tend to avoid it. In all cases the snakes failed to cross a trail scented with cloacal gland secretion.

In the next series of experiments a group of *S. dekayi* was collected from the Long Island region on April 16, 1934, and brought into the laboratory. They were placed in a refrigerator room and left there for a period of 24 hours at a temperature of 7° C. They were then placed in the usual type of cages having a layer of moist gravel on the bottom and placed in the greenhouse. These snakes showed active signs of courtship following the above procedure and were then used in the following series of trailing experiments. Since, in the previous series of experiments no sexual differentiation in respect to trailing could be established it was thought of sufficient importance to repeat the above experiments with sexually motivated snakes and to compare the trailing of these snakes with others which showed no sex responses.

Table 14 records the results as obtained with both male and female *S. dekayi* following a trail made by rubbing body integument on the substrata.

The trails were made over the same surface employed in the previous experiment and the time taken for sexually active *Storeria* may be compared with that recorded in Table 13.

From these results it can be seen that a courting male will follow an active female trail scent more rapidly than a non-courting male will follow a non-active female. This is illustrated by comparing the first series (Table 14) with the third "U series" in Table 13. During the breeding season a male will not follow or pay attention to the trail of another male. The

TABLE 14. Trailing experiments with sexually active *S. dekayi*.

| *Trailing Snakes | Trials | Trail Scent | Reaction Time in Minutes |
|------------------|--------|-----------------------------|--------------------------|
| Male N..... | 5 | Female N..... | 2.4 |
| Male N..... | 5 | Female O..... | 8.0 |
| Male N..... | 5 | Female N and Female O..... | 2.9 on Female N |
| †Male N..... | 5 | Female N and Female NC..... | 2.7 on Female N |
| Male N..... | 5 | Male N..... | No Reaction |
| Male N..... | 4 | Male O..... | No Reaction |
| Male O..... | 3 | Female N..... | 4.8 |
| Male O..... | 2 | Female O..... | 5.2 |
| Male O..... | 3 | Male N..... | 4.1 |
| Male O..... | 2 | Male O..... | 4.6 |
| Female N..... | 4 | Female N..... | 3.3 |
| Female N..... | 3 | Female O..... | 3.4 |
| Female N..... | 3 | Female N and Female O..... | 4.5 on Female N |
| Female N..... | 5 | Male N..... | 4.2 |
| Female O..... | 3 | Female N..... | 4.1 |

*Snakes used for trailing — N, sexually active.
O, sexually inactive.
†NC, trail scent from cloacal gland of inactive female.

females do not react in any different manner than females during the winter months. The experiment with cloacal gland scent was repeated and it can be seen that here again this scent is avoided. In conclusion, it may be stated that normally, irrespective of the breeding season, there is some odorous substance given off by the integument of these snakes which attracts other members of the same species, and that during the breeding season this, or more probably another substance, is given off by the female which in turn attracts the male and enables the male to distinguish sex. The nature of this substance is as yet undetermined.

The recent experiments of Kahmann and others indicate that the chief function of the flickering tongue of snakes is to pick up odorous particles in the air and carry them to Jacobson's organ. Our experiments on trailing and aggregation described above clearly indicate the olfactory organs are more important receptors than Jacobson's organs in this behavior. Although a study of the feeding behavior of snakes lies beyond the scope of this paper, it seemed desirable for comparative reasons to obtain further information on the trailing habits of the species under consideration. We, therefore, induced

a series of *S. dekayi* and *T. sirtalis* to follow a food-scented trail. Figure 11 shows an outline of a soapstone surface, the continuous line being the food-scented trail and the broken line the distilled water trail of the control.

The food used was a preparation of earthworm extract made by grinding up earthworms and filtering off the liquid after a small quantity of water had been added to the crushed earthworms. This extract was placed on a marked trail as shown above and water containing no earthworm odor was placed on another trail as illustrated. The test snake was placed in region D at the beginning of the test and a sketch of each trail made. The time required to reach the end of the stone surface BC was recorded. The Alberene stone surface used throughout the experiment was 74 cm. in width and 366 cm. in length. The food trail as outlined in the above Figure 11 was therefore approximately 424 cm. in length. In each series of tests the food and water trails were reversed. This was done so as to eliminate any chance of a snake's developing place habits. We also employed a number of different snakes of each species in each series of tests.

Figure 11 shows the trail of a normal *Storeria* over the food-scented trail. The time required to cover the trail from D to C was 9.5 minutes. This series was repeated 10 times with normal, untreated *Storeria*. The results are recorded in Table 15. In all trials the snakes reacted positively to the scented trail and the average time required for the entire series was 9.9 minutes. If the above series is compared to the following series of untreated *T. sirtalis* it can be seen from Table 15 that while the reaction was positive in all cases the time required was nearly twice that of the above series of *Storeria*. Figure 12 shows the trail of an untreated *T. sirtalis*. The time taken to transverse the route CB is much longer than that for *Storeria* while the actual trail of the *T. sirtalis* is not proportionately extended. This shows that *T. sirtalis* is much slower in following and picking up the scent.

Table 15 shows that in the case of the tongueless and the blindfolded series no significant deviation from the untreated series was evident. However, in the nose-stopped series the time consumed was greatly increased (Fig. 13). This is particularly true of the *Storeria*. In the series in which Jacobson's organ was incapacitated the time required was again increased but not so much as in the nose-stopped series (Fig. 14). This, no doubt, shows the more important significance of the nose over the Jacobson's organ in finding a food trail. When both Jacobson's organ and the nostrils were incapacitated, no reaction was evident. The snakes moved around without any regard for the food-scented trail. Sometimes they refused to move from region AD while at other times they moved from AD to CD as in Figure 15, but showed no evidence of following any trail.

From the above experiments it may be concluded that neither the tongue nor Jacobson's organ is essential for finding food or following a food-scented

TABLE 15. Sense organs involved in the finding of food.

| Series | Species | Trials | Reaction Percentage | Average Time in Minutes |
|--------|--------------------|--------|---------------------|-------------------------|
| U | <i>S. dekayi</i> | 10 | 100 | 9.9 |
| U | <i>T. sirtalis</i> | 10 | 100 | 18.0 |
| T | <i>S. dekayi</i> | 15 | 100 | 12.1 |
| T | <i>T. sirtalis</i> | 10 | 100 | 16.6 |
| B | <i>S. dekayi</i> | 10 | 90 | 10.6 |
| B | <i>T. sirtalis</i> | 10 | 100 | 20.2 |
| N | <i>S. dekayi</i> | 15 | 86 | 37.7 |
| N | <i>T. sirtalis</i> | 15 | 100 | 33.5 |
| J | <i>S. dekayi</i> | 15 | 93 | 19.0 |
| J | <i>T. sirtalis</i> | 10 | 90 | 21.0 |
| BNT | <i>S. dekayi</i> | 10 | ... | ... |
| BNT | <i>T. sirtalis</i> | 10 | ... | ... |
| TJ | <i>S. dekayi</i> | 15 | 100 | 16.0 |
| TJ | <i>T. sirtalis</i> | 15 | 93 | 24.0 |
| TJN | <i>S. dekayi</i> | 20 | ... | ... |
| TJN | <i>T. sirtalis</i> | 20 | ... | ... |
| JN | <i>S. dekayi</i> | 15 | ... | ... |
| JN | <i>T. sirtalis</i> | 15 | ... | ... |
| TN | <i>S. dekayi</i> | 15 | ... | ... |
| TN | <i>T. sirtalis</i> | 10 | ... | ... |

trail. The above function can be accomplished by the use of the olfactory organs alone. However, *S. dekayi* and *T. sirtalis*, having only the tongue and Jacobson's organ functioning, can follow the food-scented trail. The tongue alone, or Jacobson's organ alone, is inadequate in effecting a positive response to a food-scented trail. In brief, we may conclude that we have found very little evidence to support the views of Kahmann (1932). This is the more surprising in that *Storeria* and *Thamnophis* are closely related to the species of *Natrix* studied by him.

DISCUSSION

The most extensive aggregations of *Storeria dekayi* in the wild state are those taking place at the time of hibernation. The evidence presented above clearly indicates that the sensory-motor mechanisms bringing the snakes together at that time are the same as those which regulate the smaller aggregations of summer. A dropping temperature does not increase the magnitude of the aggregation response, but a snake which has been chilled moves into a warmer area when the temperature is sufficiently high to permit movement. This response brings scattered individuals into more favorable situations for

hibernations. The response to humidity is equally direct, the snakes seeking areas providing optimum conditions. When the temperature or humidity of an area deviates from the optimum the snakes tend to leave it for more favorable localities. They do not move out of this area at random, but follow the trails made by the skin of individuals of their own species. In October during both 1934 and 1935, we witnessed a movement of DeKay snakes across a street in the general direction of the hibernating area. This was on warm days (13 to 14° C.) following several colder ones when no snakes were visible. Most of the snakes were heading south and presumably along trails made by earlier arrivals.

This tendency of snakes to trail is merely a manifestation of the aggregation drive. When DeKay snakes are frightened their aggregation drive appears in its clearest form, but at other times when hunger, thirst, sex or other dispersing drives are dominant some tendency to aggregate remains. It is for this reason that the distribution of *Storeria* in any meadow or along any bank tends to be spotty.

The aggregation drive of *Storeria* and *Thamnophis* has a decided survival value. The normal response of these snakes to temperature or humidity gradients may bring them into favorable areas for wintering, but it is the tendency to trail which brings them in follow-the-leader fashion to the most suitable cavities.

During conditions of drought, the aggregation drive brings the snakes into contact with their kind with the result that less water is lost by evaporation through the skin. Aggregation also lowers the respiratory rate of these snakes conserving water which would be lost through the lungs. Allee (1931) has shown in a number of forms, particularly invertebrates, that aggregation has physiological advantages. Some of these advantages, particularly a lower metabolic rate, apply equally well to snakes (Clausen, 1934). Schuett (1933) reported a lower metabolic rate in fishes as the result of aggregation. In a later paper (Schuett, 1934) he finds that the earlier results were in error because of defective technique. Nevertheless he shows by a direct observational method that aggregation is beneficial in that it reduces activity. The aggregation drive of *Storeria* may be compared to the schooling drive of fishes, especially to that of those fishes which school only under adverse circumstances. Many of the cichlids when frightened, dash off in the same direction and form a compact group behind some shelter. Under unfavorable conditions of temperature and ionization these fishes also cluster together. The sensory components essential to hold the fish and the snake aggregates intact may differ. It has frequently been noted that fish schools such as those of the herring (Hesse and Doflein, 1914) or young catfish (Bowen, 1931) break up at night. Visual impulses therefore play as important a rôle in the formation of schools of fishes as in the aggregations

of snakes. But in the young catfish Bowen (1932) has shown that tactile impulses called forth by the reciprocal movements of the fish are also required for maintaining the school. In the snake the olfactory (or Jacobson's) organ must be properly stimulated if the aggregates are to continue. The sensory requirements in aggregating fishes and snakes may not be the same, but in both groups the tendency to cluster when frightened or when subjected to adverse conditions remains.

The hibernating den of *Storeria* and *Thamnophis* may be restricted to a single cavity or it may be widely scattered along many subterranean channels. Although most snake dens are assumed to be restricted to single cavities further work may show that the diffuse den of *Storeria* and *Thamnophis* is equally characteristic of other species. During January, 1933, we excavated a den of *Crotalus horridus* and *Agkistrodon mokasen* near Stony Point, N. Y. No less than 8 specimens of the former species and 21 of the latter were taken from an area 12 yards square. Two of each of the above species were also removed from a region 12 yards from the above area. The snakes were found singly or in groups of 2 and 3 scattered along crevices approximately 4 feet from the surface. Two *Coluber constrictor* were taken in this same area but they were not in cavities occupied by the other two species. Just as *Thamnophis* and *Storeria* were attracted to the same areas late in the fall primarily by the warmth of these localities, so the physical conditions had presumably attracted the black snakes, copperheads and rattlers to the same hillside. When few cavities are available on a particular hillside two species may hibernate together, but there is a distinct tendency at least in the species studied above for each species to seek isolation from other species.

Snakes in following trails make use of their tongues to carry the odors to the Jacobson's organs as Baumann (1929), Kahmann (1932), and others have described. Some lizards such as most Teiidae have long bifid tongues which are frequently flickered. Noble and Kumpf (1936) have shown that in spite of this important distance receptor the teiid lizard they studied still depended primarily upon its olfactory organs when seeking food. Similarly we find that in both food-seeking and companion-seeking activity, *Storeria* and *Thamnophis* are guided more by stimulations of the olfactory than by those of their Jacobson's organs.

SUMMARY

1. *Storeria dekayi* exhibits a well marked tendency to aggregate with numbers of its own species. This tendency becomes more pronounced by disturbing factors. It is present to a certain degree in some other snakes such as *Thamnophis sirtalis* and *T. butleri*.

2. Aggregation in *S. dekayi* occurs throughout the entire year with the

exclusion of the time during which gestation occurs. At this time the females are found isolated.

3. Aggregation is beneficial in that it reduces water loss. As the temperature increases the aggregation response becomes more and more beneficial.

4. There is considerable variation between species as to effectiveness of aggregation under similar conditions. This difference is correlated with the habitat preferences of the species.

5. There is a direct correlation between weight decrease and respiratory increase under isolated and aggregated conditions. Desiccation tends to reduce both weight and respiratory rate.

6. The typical aggregation response of *S. dekayi* occurs when the humidity lies between 20 and 45 per cent. The sense organs involved in the response to humidity gradients are not those involved in aggregation.

7. Aggregation in *S. dekayi* occurs normally within a more or less definite temperature range (21° to 31° C.). *T. butleri* forms typical aggregates at higher temperatures than the optimum for *S. dekayi*.

8. Vision is the primary sensory modality which enters into the aggregation response. Olfaction plays a secondary rôle, while the tongue plays little or no part in the reaction.

9. DeKay snakes are attracted by moving objects of small size. A motionless snake will not serve as a source of attraction. Color appears to have little significance.

10. Species identification is accomplished chiefly by the olfactory sense while vision enters into the response secondarily. The tongue itself plays no part in species identification.

11. The secretion of the cloacal glands does not attract. The integumental covering of the body is the source of odorous substances which serve in one case as an attraction to other individuals of the same species and in the other case to individuals of the opposite sex.

12. The olfactory organs alone are adequate sensory mechanism for food trailing in *S. dekayi* and *T. sirtalis*. The tongue and Jacobson's organs in combination make trailing possible, but either one of these structures alone is inadequate.

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